Influence of *Ecklonia radiata* patch characteristics on associated communities

by

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Declaration of originality

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Statement of Co-authorship

Chapters 2 – 5 of this thesis have been prepared as manuscripts for submission to peer-reviewed journals. The design and implementation of the research, development of methodologies, data analysis, interpretation of results and manuscript was the responsibility of the candidate but was carried out in consultation with supervisors and co-authors. These contributions are outlined below.

Chapter 2. Patch size and density of the canopy-forming kelp modify influences of ecosystem engineering on understory algal and sessile invertebrate assemblages

Craig Johnson and Jeffrey Wright contributed to the conception and design of the experiment. Matthew Cameron and Cayne Layton contributed to the development of the methodologies, and along with Masayuki Tatsumi, contributed to the implementation of field research. All authors provided comments on the manuscript.

Chapter 3. Ecosystem engineering by a canopy-forming kelp facilitates native oysters

Craig Johnson and Jeffrey Wright contributed to the conception and design of the experiment. Cayne Layton contributed to the development of the methodologies, and along with Matthew Cameron and Masayuki Tatsumi, contributed to the implementation of field research. All authors provided comments on the manuscript.

Chapter 4. Kelp patch size and density influence secondary productivity and diversity of epifauna

Craig Johnson and Jeffrey Wright contributed to the conception and design of the experiment. Graham Edgar contributed to the development of the methodologies. Matthew Cameron,

Cayne Layton and Masayuki Tatsumi, contributed to the implementation of field research. All authors provided comments on the manuscript.

Chapter 5. Canopy structure benefits fish communities but has complex effects on the recruitment of cryptobenthic species

Craig Johnson and Jeffrey Wright contributed to the conception and design of the experiment. Matthew Cameron contributed to the development of the methodologies, and along with Cayne Layton and Masayuki Tatsumi, contributed to the implementation of field research. Graham Edgar contributed to the interpretation of the results. All authors provided comments on the manuscript.

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Statement of Ethical Conduct

The research associated with this thesis abides by the international and Australian codes on human and animal experimentation, the guidelines by the Australian Government's Office of the Gene Technology Regulator and the rulings of the Safety, Ethics and Institutional Biosafety Committees of the University.

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Thesis abstract

Variability in the structure of habitat-forming species which modify local environmental conditions is likely to elicit complex effects on the associated communities and have important ramifications for the biodiversity and stability of the ecosystem. This thesis examines how kelp patch characteristics affect benthic species associated with kelp-dominated rocky reefs. Using an experimental array of artificial reefs with transplanted *Ecklonia radiata* (Australia's most dominant canopy-forming kelp species), I investigated how kelp patch size and density impacted: 1) understory algae and sessile invertebrates, focussing on turf-forming and foliose algal species as well as kelp recruitment; 2) native oysters (*Ostrea angasi*), which form critically depleted shellfish reef ecosystems and are focal species for restoration projects across Australia; 3) secondary production assessed as the growth of mobile epifaunal invertebrates which provide a critical trophic link for coastal food webs; and, 4) fish communities along with the recruitment of cryptobenthic fishes. The work found that the absence of kelp and decreasing patch size led to the proliferation of algal turfs, which primarily appeared to flourish in response to greater light availability (due to reduced shading by the canopy). Cover of algal turfs was negatively correlated with the cover of foliose algal species and native oysters, which both increased in abundance with patch size. Oysters were the most dominant benthic macroinvertebrate but were most prevalent on reefs with intermediate densities of kelp. Conversely, secondary productivity of grazing epifauna declined with kelp patch size and was reduced on reefs with intermediate kelp densities, most likely due to a negative association with the most dominant species of foliose understory algae (*Ulva*. sp.). The density of fish recruits as assessed by a standardised artificial collector declined with patch size and showed a non-linear response to kelp density in that recruitment was reduced on reefs with low and medium densities of kelp compared to reefs without kelp

or high densities of kelp. On the contrary, the abundance and species richness of fish communities were positively affected by increases in kelp patch size and high densities of kelp. Overall, these results highlight the importance of kelp patch characteristics in structuring communities spanning multiple trophic levels through modifications to abiotic and biotic ecosystem properties. The findings allude to potential consequences associated with different forms of kelp habitat decline; however, they also demonstrate that it is not only possible to establish *E. radiata* patches from transplants, but these patches will rapidly promote the (re-)establishment of the associated communities.

Chapter 1. Introduction

1.1 Background

Marine and terrestrial communities are highly variable in both space and time. Understanding community dynamics across heterogenous landscapes is a core objective in ecology and fundamental to the management of ecosystems. Ecosystems are often defined by the occurrence of habitat-forming species (e.g. trees in a forest, coral or tropical reef), which have a fundamental role in how ecosystems function. However, an important consideration when examining the influence of habitat-formers on their associated communities is the inherent patchy nature of their distribution. The concept of *patch dynamics* considers ecosystems as dynamic mosaics of interconnected patches which manifest different abiotic conditions and support different biological communities, where variability in the characteristics of patches (e.g. the size, shape, composition and configuration of patches) influences the assembly of communities (Connell and Keough 1985, White and Pickett 1985, Townsend 1989). Patch dynamics and community assembly are influenced by disturbance events which remove species and expand habitat gaps, as well as the dispersal of species amongst patches and into gaps. Although the stochastic arrival of species into patches and interactions between species can influence community development, the structural characteristics (e.g. the patch size and density) of habitat-forming species is often a key drivers of community fluctuations across patchy habitats (Dayton et al. 1992, Alvarezbuylla 1994).

The diverse communities of algae, invertebrates and fishes that inhabit coastal ecosystems are a critical components of the social, economic and ecological value associated with the marine

environment (Barbier et al. 2011). It is therefore important to understand how these communities are likely to respond to environmental change and how this may help to define conservation priorities. Forests of canopy-forming kelp dominate temperate rocky reefs globally where they provide habitat for productive and diverse ecological communities, and support a range of highly valuable ecosystem services (Steneck et al. 2002, Smale et al. 2013, Bennett et al. 2016, Coleman and Wernberg 2017). Similar to many other habitat-forming species in marine and terrestrial systems (e.g. trees, grasses, corals, mangroves etc.), kelp are considered ecosystem engineers in that they provide complex physical structure and modify local abiotic and biotic environmental conditions which support the associated communities (Jones et al. 1996, 1997, Teagle et al. 2017, Layton et al. 2019b). Additionally, kelp structure also drives species interactions such as predation, competition and facilitation, which can further influences the composition of communities (Eckman and Duggins 1991, Jones et al. 1996, Anderson 2001, Graham 2004, Benes and Carpenter 2015).

Kelp structure, in terms of patch size and kelp density, is naturally highly variable both spatially and temporally (Dayton et al. 1992). However, many kelp-dominated ecosystems also face a range of escalating environmental stressors including climate changes effects, often resulting in widespread kelp loss (Steneck et al. 2002, Ling et al. 2009a, Voerman et al. 2013, Wernberg et al. 2013, Steneck and Johnson 2014, Krumhansl et al. 2016). Together or singly, these stressors can result in kelp patches becoming more isolated, declining in size, and the density of kelp within patches being reduced. Because kelp exert strong engineering effects beneath their canopy (Steneck et al. 2002, Teagle et al. 2017), benthic communities are likely to be particularly susceptible to changes in kelp structure.

Previous research has described how the characteristics of kelp patches (e.g. patch size and kelp density) modify sub-canopy light availability, water flow, sedimentation and benthic scour by kelp laminae (Eckman et al. 1989, Kennelly 1989, Irving and Connell 2002, Connell 2005, Wernberg et al. 2005, Layton et al. 2019b) (summarised in Fig. 1.1). Increased kelp cover tends to lead to reduced light levels at the benthos, increased deposition of sediment (and other particulates) to the substratum, and reduced sub-canopy water flow (Eckman et al. 1989, Kennelly 1989, Irving and Connell 2002, Connell 2005, Wernberg et al. 2005, Layton et al. 2019b). Despite low levels of sediment deposition when kelp is absent or sparse, accumulation of sediments can be high due to elevated growth of sediment trapping algal turfs which can become dominant when shading and scour from kelp laminae is low (Filbee-Dexter and Wernberg 2018, Reeves et al. 2018, Layton et al. 2019b). Several studies have described how changes in kelp canopy characteristics and the abiotic environment can influence understory algal and sessile invertebrate assemblages (Kennelly 1989, Connell 2003, Wernberg et al. 2005, Flukes et al. 2014). Filamentous algal turfs tend to proliferate in the absence of kelp, whilst foliose species, and some sessile invertebrates are better supported beneath fuller canopies where light levels and competition from algal turfs are reduced (Kennelly 1989, Connell 2003, Wernberg et al. 2005, Flukes et al. 2014). Many mobile species such as macroinvertebrates and fishes as well as sessile suspension feeders are also likely to benefit from kelp structure through its capacity to provide food and refuge (Graham 2004, Miller and Page 2012, Miller et al. 2018). This thesis aims to build on this knowledge by experimentally examining the role of kelp patch size and density as well as ecosystem engineering in mediating benthic communities across multiple species and functional groups (Fig.1. 2).

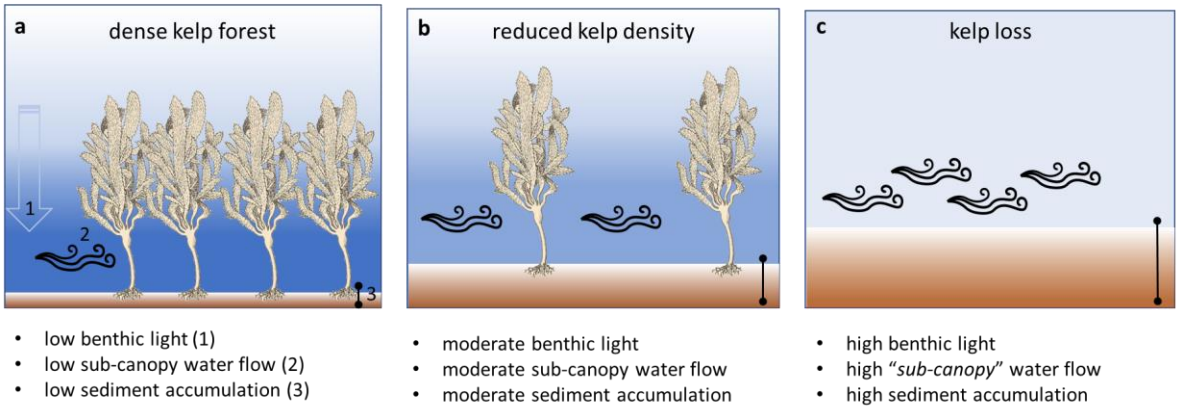

Figure 1.1 Summary of abiotic responses to changes in *E. radiata* structure based on findings by Layton et al. (2019b), which examined the same array of artificial reefs studied in this thesis.

Ecklonia radiata is the dominant canopy-forming kelp species in southern Australia and the foundation species of the 'Great Southern Reef', which is a network of rocky reefs spanning the southern coastline of Australia which has tremendous social, economic and ecological value (Bennett et al. 2016). Similar to many kelp forests globally, the canopy structure of *E. radiata* varies considerably across its distribution in Australia with notable and relatively recent loss of kelp cover recorded in Western Australia (Wernberg et al. 2013, Wernberg et al. 2016), South Australia (Connell et al. 2008), Victoria (Shepherd et al. 2009), Tasmania (Ling et al. 2009a, Johnson et al. 2011) and New South Wales (Vergés et al. 2016) due to a range of stressors (e.g. grazing by sea urchins, sedimentation, decline in water quality, marine heatwaves etc.). Severe kelp loss can lead to alternative stable states for kelp forest ecosystems. For example, a *barren ecosystem stat*e can be created through high levels of grazing by sea urchins. This ecosystem state is characterised by the near complete absence of macroalgae and especially low levels of productivity and biodiversity (Steneck et al. 2002, Ling 2008, Filbee-Dexter and Scheibling 2014, Steneck and Johnson 2014). Alternatively, a *turf-dominated state* may occur through others forms of kelp loss, especially when

accompanied by high nutrients (Connell et al. 2008). These systems occur when filamentous algal turfs dominate the reef substratum and suppresses that establishment of other macroalgae (Kennelly 1987a, Gorgula and Connell 2004, Isæus et al. 2004, Connell Sean and Russell Bayden 2010, Wernberg et al. 2016, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). Both degraded ecosystem states are likely to have widespread adverse effects on the productivity and biodiversity of communities more broadly (Ling 2008, Filbee-Dexter and Wernberg 2018).

This thesis examines the communities that developed on a suite of artificial reefs in which the patch size and density of *E. radiata* were manipulated systematically as a means of assessing how the structure of this kelp species along with the engineered environmental conditions determine community responses. Use of artificial reefs with kelp transplants allowed a precise means to manipulate kelp structure, whilst (to a greater extent) keeping other factors that can influence communities (i.e. depth, slope, other influential species) relatively constant. Although artificial reefs may not necessarily be a perfect surrogate for natural rocky reef (e.g. there may be differences in species assemblages), these reefs were intended to highlight general mechanisms and responses pertaining to influences of kelp structure on communities that are also likely to play out in other systems. In addition to helping determine how different kelp patch characteristics are likely to influence communities, this research also aims to highlight community responses to different forms of kelp loss, and document how communities proceed to establish in response to the (re-)establishment of kelp habitat on natural and artificial structures.

1.2 Thesis structure

The principal objectives of this thesis are to determine how *E. radiata* patch size and density influence:

1) understory algae and sessile invertebrate communities with a particular focus on filamentous algal turfs, foliose species, and *E. radiata* recruitment (chapter 2);

2) the recruitment of the native oyster *Ostrea angasi* and potential implications for the restoration of *O. angasi* oyster reefs, which is a critically depleted reef forming oyster species (chapter 3);

3) secondary productivity and biodiversity associated with small grazing epifauna that are an important trophic link in coastal food webs (chapter 4), and;

4) fish communities and the recruitment of cryptobenthic fishes (chapter 5).

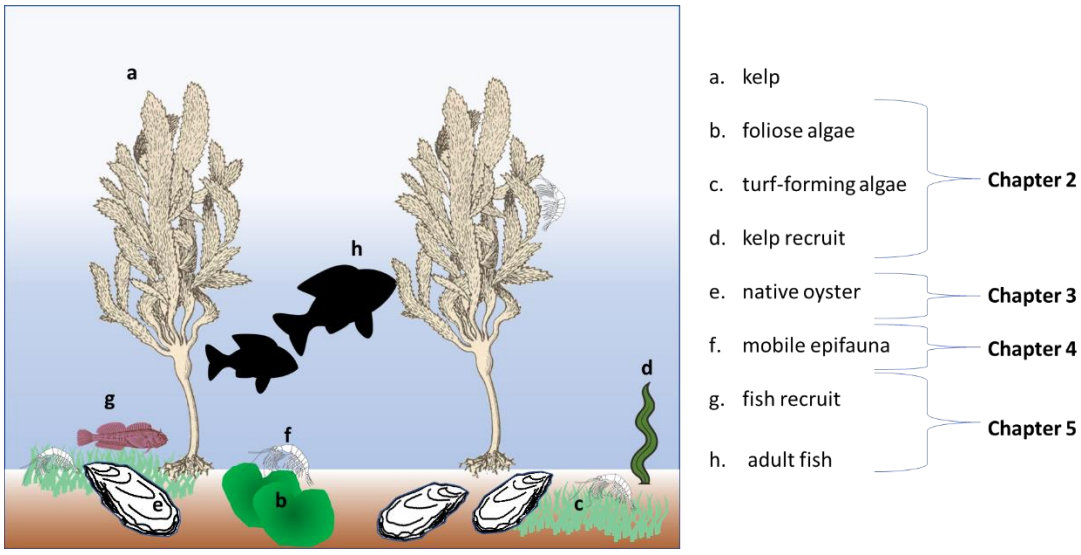

Figure 1.2 Representation of a kelp forest community showing the components of the community investigated in this thesis. Note that mobile macroinvertebrates such as sea urchins were not considered in this thesis despite their capacity to influence the ecosystem.

These aims (Fig. 1. 2) underpin field experiments conducted over two years using an array of experimental artificial reefs spanning a range of sizes (0.12 – 7.68 m^2) onto which fully developed adult *E. radiata* sporophytes were transplanted at particular densities (0 – 16 kelps per m^2). Transplanting adult kelps to the newly established reefs and maintenance of the adult kelp populations on each reef over the course of the experiment were the only manipulations undertaken. The integrated findings and implications of this research are discussed in chapter 6.

Note that each chapter has been prepared as a stand-alone paper for submission to a journal. Thus, inevitably there is some overlap in content, particularly in the Introduction and Methods sections of the chapters. This format for a PhD thesis is permitted by the University of Tasmania. A brief outline of each chapter follows:

Chapter 2. Patch size and density of canopy-forming kelp modify influences of ecosystem engineering on understory algal and sessile invertebrate assemblages

Experiments described in this chapter determined the effect of different *E. radiata* patch sizes and densities on the composition of understory algal (focusing on the abundance of algal turfs, foliose algae, and *E. radiata* recruits) and sessile invertebrate communities. The importance of abiotic and biotic kelp engineering effects in influencing the abundances of foliose algae, turfing algae, sessile invertebrates and *E. radiata* recruitment are also considered. Major hypotheses tested: *E. radiata* patch size and presence would reduce the cover of 1) turf algae and increase the abundance of 2) foliose algae, 3) sessile invertebrates, and 4) *E. radiata* recruitment.

Chapter 3. Ecosystem engineering by a canopy-forming kelp facilitates recruitment of native oysters

Experiments described in this chapter determined the effects of *E. radiata* patch size and density on the recruitment and persistence of *Ostrea angasi.* We additionally considered the potential influences of kelp engineering in determining *O. angasi* abundance. Results are discussed in terms of the potential implications for restoration of *O. angasi* reef ecosystems which are a critically depleted ecosystem in Australia. Main hypothesis tested: *E. radiata* patch size and presence would increase the recruitment of *O. angasi*.

Chapter 4. Kelp patch size and density influence secondary productivity and diversity of epifauna

Experiments described here demonstrate how changes in *E. radiata* patch size and density relate to secondary productivity, and the biodiversity of free-living epifaunal meso-invertebrates associated with the understory. The role of invertebrate feeding strategy as well as abiotic and biotic factors in determining secondary productivity were also considered. The implications of the results for the productivity and biodiversity of coastal food webs are discussed. Main hypothesis tested: *E. radiata* patch size and presence would 1) increase the species richness and diversity of epifauna but 2) reduce epifaunal secondary productivity.

Chapter 5. High densities of kelp attract fishes other than recruiting cryptobenthic species

This chapter demonstrates the relationship between *E. radiata* patch size and density and the associated communities of fishes along with the recruitment of cryptobenthic fish species. The potential causes for these associations and possible implications of kelp decline or the (re-)establishment of kelp on fish communities are discussed. Main hypothesis tested: *E.*

radiata patch size and presence would increase 1) the abundance and species richness of fishes, and 2) the recruitment of cryptobenthic fishes.

Chapter 6. General Discussion

In the final chapter, I integrate the results across the study to consider how the community as whole is likely to respond to modification of kelp habitat characteristics and discuss some study limitations. I then provide discussion on the broader implications of the community response, especially in relation to predicted trajectories of kelp forest communities subjected to different forms of habitat degradation, implications for the stability of the ecosystem, and the potential for the findings of the work to inform marine habitat restoration.

Chapter 2. Patch size and density of the canopy-forming kelp modify influences of ecosystem engineering on understory algal and sessile invertebrate assemblages

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2.1 Abstract

Ecosystem engineers are important in shaping the composition of associated communities, including the abundance of species which exert additional influences on the ecosystem. Using an array of 28 artificial reefs supporting transplants of a dominant canopy-forming kelp (*Ecklonia radiata*) representing seven patch sizes (0.12 - 7.68 m^2) crossed with four kelp densities (0, 4, 8 and 16 individuals m^{-2}), we determined how differences in the patch size and density of this ecosystem engineer influenced the associated understory assemblages, including the abundance of turf algae, foliose algae and sessile invertebrates. We then determined how abiotic and biotic factors modified by *E. radiata* related to the abundance of these functional groups and *E. radiata* recruitment. Decreasing patch size and absence of kelp led to the proliferation of turfs, whilst foliose algae and invertebrates were dominant on larger reefs with kelp, where intermediate densities of kelp supported the highest abundance of foliose algae. We postulate that benthic light was the most important factor positively influencing turf cover, which in turn suppressed foliose algae. Adverse effects of light and sediment deposition best explained the cover of invertebrates. Contrary to expectation, understory species had little effect on the density of *E. radiata* recruits, which instead was strongly correlated with the abundance of transplanted kelp on each reef. These results highlight the capacity of *E. radiata* to influence major functional groups within the sub-canopy via abiotic ecosystem engineering and through control of turfs and indicate that the negative effect of understory algae on kelp recruitment may be context specific.

Key words: ecosystem engineer; foliose algae; kelp; understory; recruitment; sessile invertebrate; turf algae

2.2 Introduction

Different patch sizes and densities of habitat-forming ecosystem engineers may profoundly affect the associated communities and the stability of the ecosystem by altering how these species influence local environmental conditions (Tsuchiya and Nishihira 1985, Bennett and Wernberg 2014, Flukes et al. 2014, Layton et al. 2019b). Canopy-forming algae (of the orders Laminariales and Fucales, hereafter collectively referred to as 'kelp') on rocky reefs are foundation species that support extremely productive and diverse marine ecosystems (Steneck et al. 2002, Coleman and Wernberg 2017). Kelp support the establishment and persistence of ecological communities via their role as ecosystem engineers, providing physical structure and exerting strong influences on the abiotic and biotic environment (Steneck et al. 2002, Teagle et al. 2017), with the structure of kelp being integral to their faciliatory role (Wernberg and Goldberg 2008).

Kelp patch size and density vary naturally at both local and regional scales (Dayton 1985b, Wernberg 2009, Wernberg et al. 2011), but both are being increasingly modified through escalating effects of environmental stressors, including increasing temperature, sedimentation, overgrazing etc. (Steneck et al. 2002, Harley et al. 2012, Wernberg et al. 2013). Habitat degradation manifesting in declining kelp patch size and canopy density will transform the abiotic environment beneath the canopy leading to an increase in the availability of light at the benthos, water flow and retention of sediments, whilst particle deposition rates are likely to decline; however, kelp density on its own may be unrelated to flow (Wernberg et al. 2005, Layton et al. 2019b). Kelp laminae also scour the benthos in surge (Kennelly 1989), abrading understory species and resuspending sediments, although it is unclear how scour will change with declines in patch size and density. These abiotic factors

are highly important to the recruitment and development of understory algal and sessile invertebrate assemblages (Kennelly 1987c, 1989, Duggins et al. 1990, Clark et al. 2004, Wernberg et al. 2005, Flukes et al. 2014), which further shape kelp forest community dynamics (Arkema et al. 2009). Additionally, due to the localised recruitment of many kelp species, a modified abiotic and biotic sub-canopy environment is likely to provide a feedback mechanism affecting kelp population dynamics (Dayton 1985a, Kennelly 1987a, Thrush et al. 2008, Gorman and Connell 2009, Harley et al. 2012, Tatsumi and Wright 2016).

Intact kelp canopies block out in excess of 90 % of incident light from reaching the benthos (Gerard 1984), which drastically inhibits the growth of many understory algae, which may otherwise out-compete kelp recruits in some circumstances (Kennelly 1987a, Gorman and Connell 2009, Tatsumi and Wright 2016). Kelp forests also disrupt water flow, which can increase the deposition of particulates to the benthos positively influencing sediment deposition rates as well as the delivery of nutrients and the settlement of larvae to the substratum (Jackson and Winant 1983, Eckman et al. 1989, Hondolero and Edwards 2017). Low flow rates also concentrate chemical cues for larval settlement (Abelson and Denny 1997) and reduce the risk of dislodgement of recruits following settlement (Norton 2009). Even though kelp forests may have elevated sediment deposition rates compared to their surroundings (Eckman et al. 1989), the amount of sediment that accumulates on the benthos can paradoxically be lower (Layton et al. 2019b). This may result from kelp laminae scouring the benthos and removing sediments directly (Kennelly 1989) or through scour and other influences of kelp negatively affecting the abundance of sediment trapping turfs (Connell et al. 2014). Scour and sediment stress can also supress the establishment of other algal species and sessile invertebrates (Velimirov and Griffiths 1979, Kennelly 1989, Irving and Connell 2002, 2006). The composition of understory communities and recruitment of the next

generation of canopy-formers ultimately depends on interactive effect of multiple biotic and abiotic factors.

Ecklonia radiata is the dominant kelp species across southern Australasia and is the foundation species of the 'Great Southern Reef', a network of reefs spanning the entire southern coast of Australia which has enormous social, ecological and economic importance (Bennett et al. 2016). Similar to many other kelp forests globally, the canopy structure of *E. radiata* in Australia varies considerably across its distribution with notable and relatively recent loss of kelp cover reported in Western Australia (Wernberg et al. 2013, Wernberg et al. 2016), South Australia (Connell et al. 2008), Victoria (Shepherd et al. 2009, Kriegisch et al. 2016), Tasmania (Ling et al. 2009a, Johnson et al. 2011) and offshore islands in New South Wales (Vergés et al. 2016) caused by a range of stressors. The effects of *E. radiata* canopy loss on understory assemblages have been well studied (Kennelly 1987b, 1989, Melville and Connell 2001, Irving and Connell 2006), and we know some of the effects of declining density (Kennelly 1987c, Duggins et al. 1990, Toohey and Kendrick 2008, Flukes et al. 2014). However, although *E. radiata* patch size varies over its range (Connell and Irving 2008) and could be diminishing in the southern part of its distribution due to the southward expansion of sea urchins (Ling et al. 2009b), we know little about the effects of patch size on understory communities nor the interactive effects of reductions in kelp patch size and density. Anticipating the repercussions of various manifestations of kelp loss (e.g. loss of patch size and loss of density) requires better understanding of how environmental covariates affected by kelp structure shape key functional groups. This understanding may also inform strategies to help restore degraded/modified kelp forest ecosystems in coastal areas (e.g. by varying kelp structure to promote biodiverse and robust communities).

The loss of *E. radiata* often gives rise to an increased dominance of turf algae (Kennelly 1987b, Wernberg et al. 2016), which consist largely of low growing filamentous species that often thrive under high benthic light levels, high sediment deposition rates and low scour (Connell 2005, Irving and Connell 2006, Russell 2007). The ability of kelp to suppress the development of turfs through canopy shading, the removal of sediments (which often stress other algal species), and damage to small understory algae by scour, is crucial for the maintenance of robust and diverse kelp beds (Connell et al. 2014, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). Due to their tendency to trap sediments (Connell et al. 2014) and possibly by forming a chemically distinct boundary layer (Layton et al. 2019a), the proliferation of algal turfs is likely to inhibit the establishment of other species (Connell 2003, Arkema et al. 2009), including kelp recruits (Kennelly 1987a, Gorman and Connell 2009).

A less intense increase in sub-canopy light caused by E. radiata canopy thinning is also likely to result in a shift in the composition of understory communities (Toohey and Kendrick 2008), potentially leading to increased dominance of foliose algal species and a reduced abundance of some sessile invertebrates and encrusting algae (Wernberg et al. 2005, Flukes et al. 2014). Although an increase in sub-canopy light levels associated with declining kelp density on its own will likely benefit some foliose algae, corresponding changes in flow, sedimentation and turf algae cover may lead to variable effects across the algal community (Wernberg et al. 2005). Meanwhile, increased light and sedimentation are likely to cause a decline in sessile invertebrate cover (Duggins et al. 1990, Connell 2003).

Within relatively pristine systems, kelp tend to recover rapidly following small-scale canopy loss, with latent recruits quickly able to take advantage of the increased sub-canopy light

levels and rapidly fill canopy gaps (Johnson and Mann 1988, Kennelly and Underwood 1993, Carnell and Keough 2014). However, prolonged degradation which causes changes to the composition of understory species, especially the prevalence of turf algae (Kennelly 1987a, Gorman and Connell 2009) and foliose algae (Tatsumi and Wright 2016), may inhibit this mechanism of resilience.

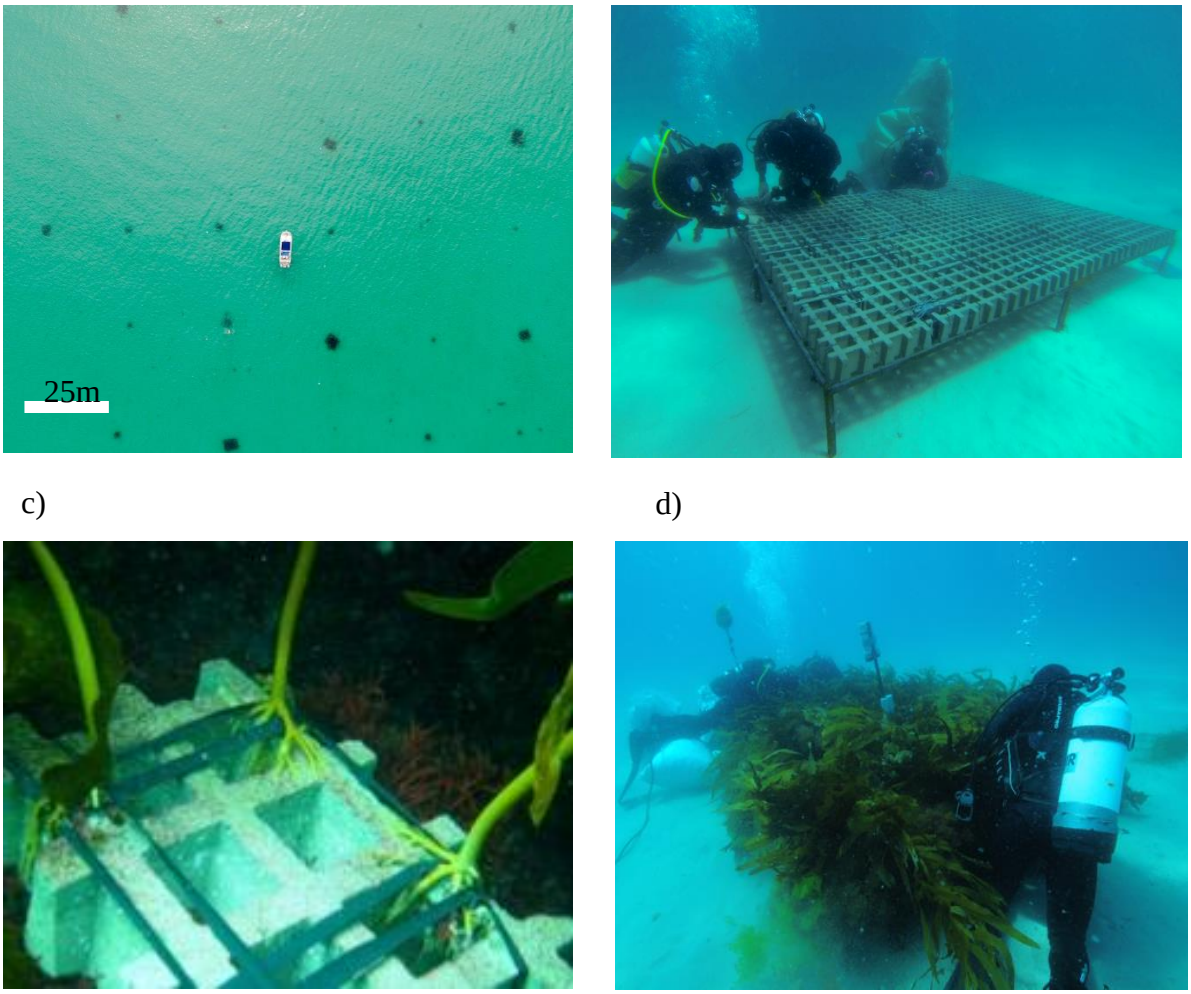
We created an array of 28 artificial reefs supporting transplanted *E. radiata* of different patch sizes and densities to investigate the separate and combined effects of kelp patch size and density on ecosystem engineering of sub-canopy algae and sessile invertebrates over two years. Using these reefs we tested the following hypotheses: H1 – that reductions in kelp cover positively influence turfs, H2 – that an intermediate level of kelp cover is most beneficial for foliose algae and H3 – that reductions in kelp cover will negatively influence sessile invertebrates. Because our focus was on the role of ecosystem engineering in shaping understorey assemblages, we further aimed to determine the importance of various abiotic and biotic factors (related to kelp structure) in driving the abundance of turfs, foliose algae, sessile invertebrates, and the density *E. radiata* recruits. In doing so, we also tested the hypothesis H4 – that understory algae negatively influence kelp recruitment and therefore could provide a feedback mechanism which reinforces declines in kelp forest ecosystems. Although these reefs will be different to natural reefs, they allow a strong test of engineering effects of *E. radiata* independent of other factors such as topography, depth, surrounding communities (especially sea urchin grazers) etc. that will vary on natural reefs. We use original data in combination with measurements of abiotic factors and *E. radiata* recruitment from Layton et al. (2019b) (quantified across the same experimental reefs), in which the relationship between abiotic factors and recruitment was not quantified.

2.3 Materials and methods

2.3.1 Study system

Experiments were conducted off the west coast of Maria Island in south eastern Tasmania, Australia (-42.64693,148.01481), using an array of artificial reefs with transplanted *Ecklonia radiata* described in Layton et al. (2019b). The reefs, which were constructed of concrete pavers and supported by a steel frame were deployed across a flat sandy substratum of uniform depth (6.5 m) and over 1.5 km away from the nearest natural reef. The reefs were deployed in an approximately square grid (Fig. 2.1a) with distances between reefs of 25 m. An analysis of covariance was applied across 28 individual reefs, which represented seven different patch sizes (0.12, 0.24, 0.48, 1.08, 1.92, 4.32 and 7.68 m^2) crossed with four kelp densities (0, 4.1, 8.2 and 16.4 kelp m^{-2}). The kelp densities represent the average density of adult kelp on nearby reefs (8.2 kelp m^{-2}), half that density (4.1 kelp m^{-2}), twice that density (16.4 kelp m^{-2}) and no kelp as controls for background levels of recruitment. All these densities (hereafter referred to as zero, low, medium and high kelp densities in order of increasing density) exist naturally in heterogeneous kelp populations. The reef infrastructure was deployed in December 2014 and kelp were first transplanted to the reefs in January/February 2015. Experiments took place over the next two years (until December 2016) and during this time kelp densities were maintained by replacing any kelp losses with fresh transplants at regular intervals (approximately every six weeks) from a nearby collection site. Briefly the transplant methodology involved the collection of healthy adult kelp from the collection site and securing intact holdfasts to reef infrastructure (Fig. 1.1b) with thick rubber bands (Fig. 1.1c) (Layton et al. 2019b). Communities of other algae, fish and invertebrates were allowed to establish naturally on the reefs (Fig. 1d shows a completed reef 1 year after deployment).

a) b)



c) d)

Figure 2.1. Images highlighting **a)** the arrangement of experimental reefs, **b)** the construction of the experimental reefs, **c)** kelp transplantation to concrete pavers, **d**) the experimental reefs after an establishment period of ~12 months.

2.3.2 Development of turf algae and foliose algae over time

Photo quadrats were used to assess the development of the understory algae on each reef. Images were captured with the camera (Canon Powershot G16 with underwater housing) positioned below the kelp canopy with *E. radiata* lamina temporarily pushed aside so that they did not obscure the understory. Photo quadrats captured 0.12 m^2 of reef surface and were taken at 1 - 4 different randomised locations depending on reef size (1 photo from 0.12 &

0.24 m^2 reefs, 2 photos from 0.48 m^2 reefs, and 4 photos from all larger reef sizes). Photos were taken on five occasions: in May, July and September 2015 and January and December 2016 (5, 7, 9, 13 & 24 months after the reefs were deployed). The percentage cover of turf-forming and foliose algae was determined from the images using CPCe software (Kohler and Gill 2006) that assigned 49 regularly spaced points on the images (results were averaged when multiple images of the same reef were captured). Foliose algae consisted of all foliose and corticated foliose growth forms (Steneck and Dethier 1994), while turf algae consisted of multi-species assemblages dominated by filamentous and branching algae, and which were low-growing, densely packed, and had a tendency to trap and hold sediments.

2.3.3 Understory communities at the conclusion of the experiment

At the final time of sampling (December 2016), photos were taken using a slightly modified method to that described above so that photos could be matched to subsequent destructive sampling. For these final photos, we captured either the entire surface area of the reef (for reefs < 1 m^2) or, for reefs > 1 m^2, a 1 m^2 area determined from a quadrat positioned in their north-east corner. These areas were captured through multiple images capturing 0.12 m^2 of reef surface area. These images were then analysed in the same manner described previously. Following taking the photos, all algae in the photographed area were carefully removed from the reef with the help of scrapers, a wire brush and an air-driven venturi suction sampler fitted with collection bags with a 500 µm mesh. These samples were frozen and stored for later analysis. After algae were removed, a second set of photos was taken of the same area from which the algae were removed, capturing the sessile invertebrates beneath the understory algae, the cover of which was analysed in the same manner as other photo quadrats.

Frozen algal samples were gently thawed and sorted by species into individual pre-weighed aluminium trays. The dry weight of each species was determined by placing the samples into a 60 °C oven for 48 hours (or until constant mass was achieved). The biomass of the different functional groups (Steneck and Dethier 1994) was then determined by pooling the constituent species. Total species richness, Shannon-diversity and the community structure of algae and invertebrate assemblages were determined. For algae, Shannon-diversity was calculated using biomass (dry weight), while for invertebrates it was calculated using percentage cover (determined from the photo quadrats) of eight taxonomic groups (solitary ascidians, colonial ascidians, bryozoans, sponges, hydroids, barnacles, mussels and oysters).

2.3.4 Abiotic factors and E. radiata recruitment

Abiotic measurements from the reefs and *E. radiata* recruitment data are from Layton et al. (2019b) which measured: sub-canopy irradiance (as a percentage of above canopy irradiance, using a LI-COR light sensor), sub-canopy flow (as a percentage of above canopy flow, determined by clod card dissolution rates), sub-canopy sediment deposition (as a percentage of the above canopy rate of deposition) determined using sediment traps placed above and below the canopy of each reef, and sediment accumulation (as the depth of accumulated sediments of the reef surface). Light was measured in November 2015, flow and sediment deposition measurements were averaged across multiple seasons in 2015, and sediment accumulation measurements were averaged across September 2015 and January 2016. *E. radiata* recruitment per unit area was assessed by counting the total number of visible stage 1, 2, and 3 recruits (Kirkman 1981) collected from each reef in the destructive sampling at the end of the experiment (December 2016). Briefly, abiotic data showed declines in irradiance, water flow, and sediment deposition, but an increase in sediment accumulation with

increasing kelp patch size and density and *E. radiata* recruit abundance increased with reef size and adult density (Layton et al. 2019b).

2.3.5 Analyses

The effects of density (fixed factor) and patch size (covariate) on the percentage cover of turfs and foliose algae were analysed using Analysis of Covariance (ANCOVA) based on routines in R (version 3.2.4). Three separate one-way ANCOVAs (at 7, 13 and 24 months post deployment, determined *a priori*) were conducted for both turf and foliose algae percentage cover. ANCOVA was also used to assess the effects of patch size and density on the cover of sessile invertebrate as well as the richness and diversity of algal species and invertebrate functional groups at the end of the experiment. Model assumptions were checked by diagnostic plots (for normality, linearity and homoscedascity), model residuals (for linearity and homoscedascity) and the Shapiro-Wilks normality test. Data transformations were determined from the λ coefficient at the maximum log-likelihood plot produced using the Box-Cox procedure. The covariate (patch size) was $\log_2$ transformed as patch size increased on (approximately) a $\log_2$ scale and this improved conformity to the test assumptions. Homogeneity of slopes was tested by fitting the saturated model including the interaction term, before the unsaturated model without the interaction term was fitted when this assumption was upheld. If the saturated model did not show homogeneity of slopes, the least homogenous treatment was omitted and the analyses was re-run following the same procedure. Figures using untransformed data were produced using the *ggplot2* package. Where a significant effect of kelp density was detected, pairwise comparisons of covariate adjusted means with a Bonferroni adjustment of significance (to correct for multiple testing) were performed (Quinn and Keough 2002) using the *lsmeans* and *multcomp* packages.

The community structure of algal species and invertebrate functional groups were analysed using PRIMER 6. Separate multi-dimensional scaling (MDS) plots and canonical analysis of principal coordinates (CAP) plots 'pooling' across different reef sizes were undertaken for algae and invertebrates. Analyses used Bay-Curtis similarity matrices using fourth root transformed algal biomass data and log transformed invertebrate percentage cover data. Only data from the four largest reef sizes was used (of which the same reef area was sampled (1 m^2)) in order to control for the effect of sampling area (which appeared to obscure patch size and kelp density effects). Differences in the community structure between kelp density and patch size were assessed using permutational multivariate analysis of variance (PERMANOVA). Given the limited range of reef sizes used in the investigation, both patch size and kelp density were treated as fixed factors and due to a lack of replication (at the interaction level), we could not assess the significance of the interaction between kelp patch size and density. To assess the reliability of the PERMANOVA results, we also tested homogeneity of dispersion (deviations from centroid) grouping across kelp density using PERMDISP.

Regression and multiple regression was used to investigate the potential influence of abiotic (light, flow, sediment deposition and sediment accumulation) and biotic factors (percentage cover of turf algae, foliose algae, and sessile invertebrate) on the cover of turfs, foliose algae and sessile invertebrates, and on the density of *E. radiata* recruits at the end of the experiment (excluding biotic predictors when they were the same as the response variable being investigated). Separate analyses were performed for each response variable, where the effects of abiotic and biotic predictor variables were analysed separately and in combination. We also investigated the effect of the number of adult kelp present on the reef on the density of *E. radiata* recruits. For *E. radiata* recruitment analyses, only the reefs where natural recruitment

was detected were used. Normality, linearilty and homogeneity of variance of variables were investigated with a scatterplot matrix and diagnostic plots (as outlined for ANCOVA) and data was transformed to meet test assumptions. Multi-colinearlity of predictor variables was investigated through pairwise correlations and examination of the variance inflation factor. All biotic predictor variables were highly correlated, and light was highly correlated with percentage cover of turfs. To address multi-collinearity, the influence of biotic factors on understory functional groups and *E. radiata* recruitment was examined through comparing the fit of single-term regression models (one for each biotic predictor). Examination of abiotic factors involved comparing the fit of all possible models containing abiotic factors for each response variables (Quinn & Keough 2002) using AIC (Akaike's information criterion) and the *leaps* package in R. The same process was followed for examination of biotic and abiotic factors together, however, the optimisation procedure was performed multiple times, separately including each correlated term minus the term(s) it was correlated with. We then selected the model with the greatest explanatory power overall. Hierarchical partitioning was then used to determine the independent contribution of each of the predictor variables considered in each multiple-regression model using the *hier.part* function. We then determined the likelihood that the independent contribution could be due to chance by performing a randomization test and assessing the significance of the *Z* scores at the 95 % confidence level.

2.4 Results

Consistent with our hypotheses, turfs were negatively related to kelp presence and patch size, whilst foliose algae and sessile invertebrates were positively related to kelp presence and patch size. The abundance of these functional groups was strongly associated with sub-

canopy light and other understory algae, whilst *Ecklonia radiata* recruitment was strongly associated with the number of transplanted adult kelp.

2.4.1 Effect of kelp patch size and density on turfs

Turf algae rapidly colonised the reefs and maintained a consistent level of cover for the duration of the two-year experiment, however, the appearance of this functional group changed over time with turfs increasing in height, density and complexity through the course of the experiment (Figs 2.2a, 2.2b). Turf cover decreased with patch size on reefs supporting adult kelp, but remained high on reefs without kelp at all times (Fig. 2.3, Table 2.1). Larger reef sizes (> 1.08 m^2) without kelp had 2 - 3 times more turf cover than similarly sized reefs with kelp (generally > 50 % vs. < 25 % cover). Turf cover decreased significantly with patch size in July 2015 and January 2016, and there was a significant effect of kelp density at both times, but the only significant pairwise comparison occurred in January (zero > high). There was a significant patch size x kelp density interaction in December 2016.

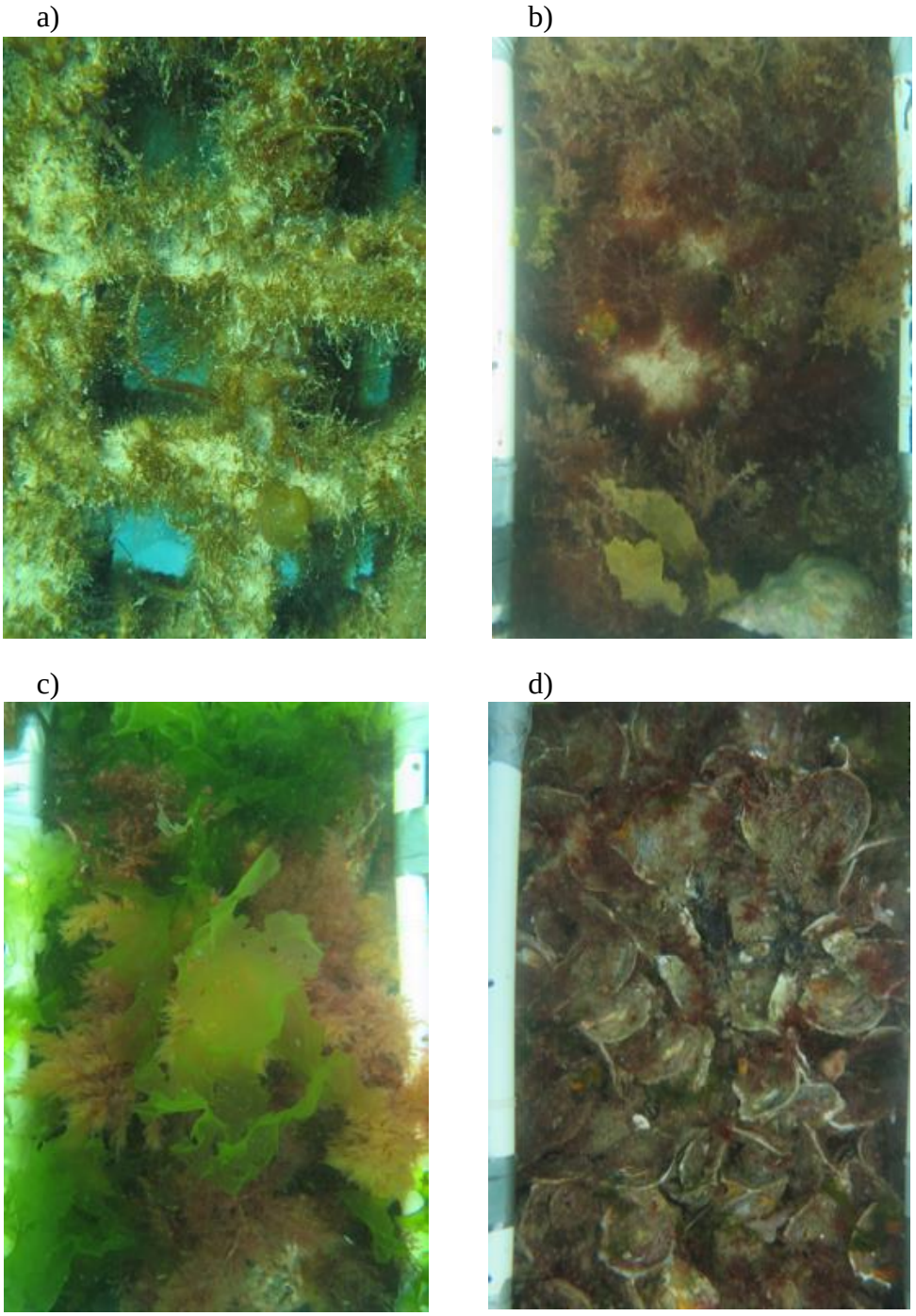


Figure 2.2. Photos on 4.32 m^2 reefs of understory assemblages. **a)** turf-dominated understory on reef with no kelp, May 2015), **b)** turf-dominated understory on reef with no kelp, December 2016), **c)** foliose algae dominated understory on reef with the medium kelp density, December 2016, and **d)** *O. angasi* dominated understory, with the picture taken after destructive sampling of the understory algae on reef supporting the medium kelp density, December 2016).

model	factor	SS (df)	F-value	p-value	Post-hoc
TURF % COVER					
July 2015	kelp density	104.38 (3, 23)	3.35	**0.036 ***	zero = low = medium
$(x)^{0.63}$					= high
	$\log_2$(patch size)	63.24 (1, 23)	6.10	**0.021 ***	
January 2016	kelp density	75.75 (3, 23)	3.56	**0.030 ***	zero > high
$(x)^{0.57}$	$\log_2$(patch size)	157.47 (1, 23)	22.20	**< 0.001 ***	
December 2016	kelp density *	326.45 (3, 20)	3.27	**0.042 ***	
$(x)^{0.77}$	$\log_2$(patch size)				
December 2016	kelp density	13.16 (2, 17)	0.63	0.544	
(no zero	$\log_2$(patch size)	260.87 (1, 17)	24.98	**< 0.001 ***	
density)					
$(x)^{0.63}$					
FOLIOSE % COVER					
July 2015	kelp density	6.70 (3, 23)	7.70	**< 0.001 ***	zero < low= medium
$(x)^{0.27}$					= high
	$\log_2$(patch size)	9.89 (1, 23)	34.11	**< 0.001 ***	
January 2016	kelp density	1.96 (3, 23)	3.47	**0.033 ***	zero < low
$(x)^{0.18}$	$\log_2$(patch size)	8.48 (1, 23)	44.90	**< 0.001 ***	
December 2016	kelp density	15.42 (3, 23)	5.48	**0.005 ***	zero < low = medium
$(x)^{0.35}$	$\log_2$(patch size)	4.24 (1, 23)	4.51	**0.044 ***	

Table 2.1. Results of ANCOVA models testing the effects of kelp density and patch size on the cover of turf algae and foliose algae on three sampling occasions. Model outputs are either from full models where there was a density x patch size interaction or unsaturated models after confirming homogeneity of slopes. Response variable transformations are shown in the model column. The covariate (patch size) was $\log_2$ transformed. Significant p values from the ANCOVA are bolded and denoted with *****. Significant post-hoc pairwise comparisons are indicated in the Post-hoc column.

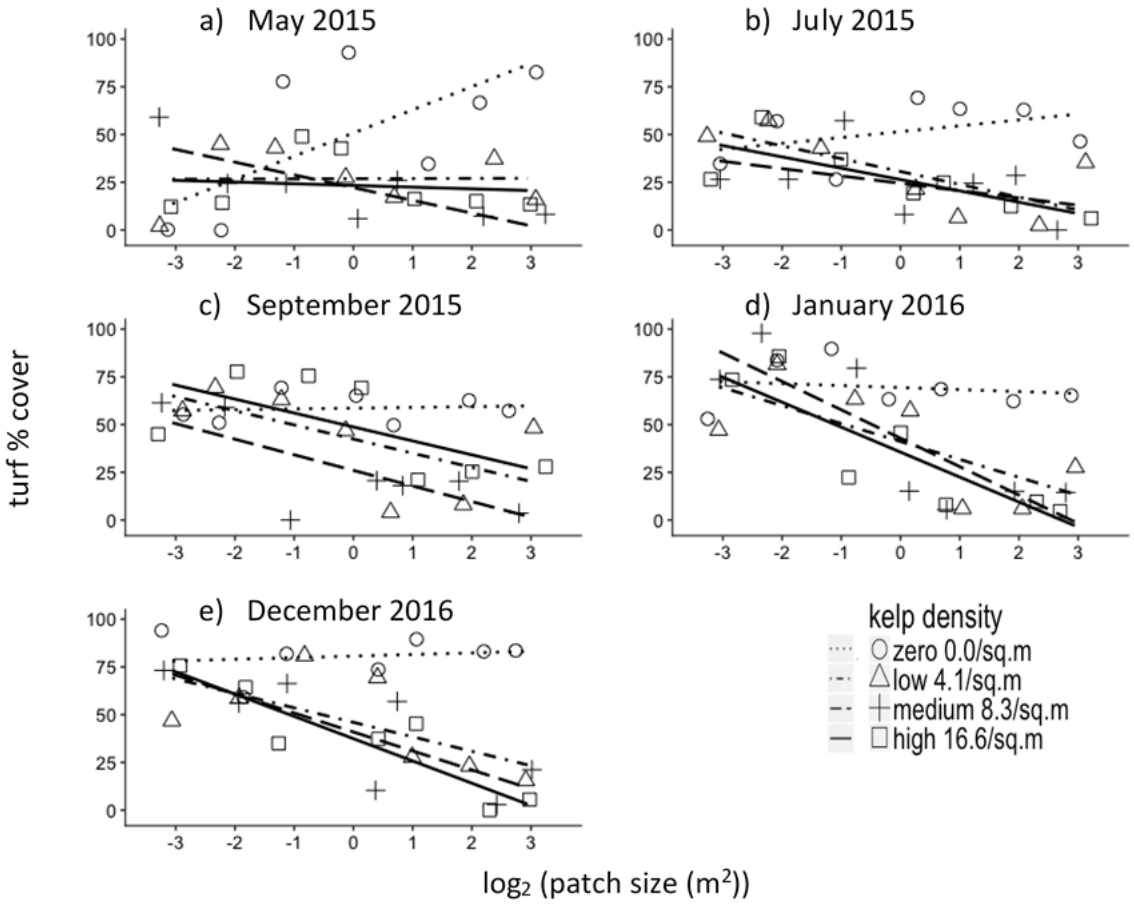


Figure 2.3. Percentage cover of turf algae on the different patch size and kelp density on five sampling occasions (5, 7, 9, 13 and 24 months after installation of the reefs).

2.4.2 Effect of kelp patch size and density on foliose algae

Foliose algae took longer to establish than turfs and always increased significantly with patch size (Fig. 2.4, Table1). Foliose algae cover was greatest on larger reefs supporting kelp in September and January, where it covered approximately 75 % of the reef surface (Fig. 2.2c shows a typical understory dominated by foliose algae), approximately three times higher than foliose algal cover on equivalent sized reefs without kelp. Reefs without kelp supported significantly less foliose algae than reefs with a low density of kelp in July 2015, January 2016 and December 2016, had less foliose algae than reefs supporting medium densities of

kelp in July (2015) and December (2016), and had less foliose algae than reefs supporting high densities of kelp in July (2015) (Table 1).

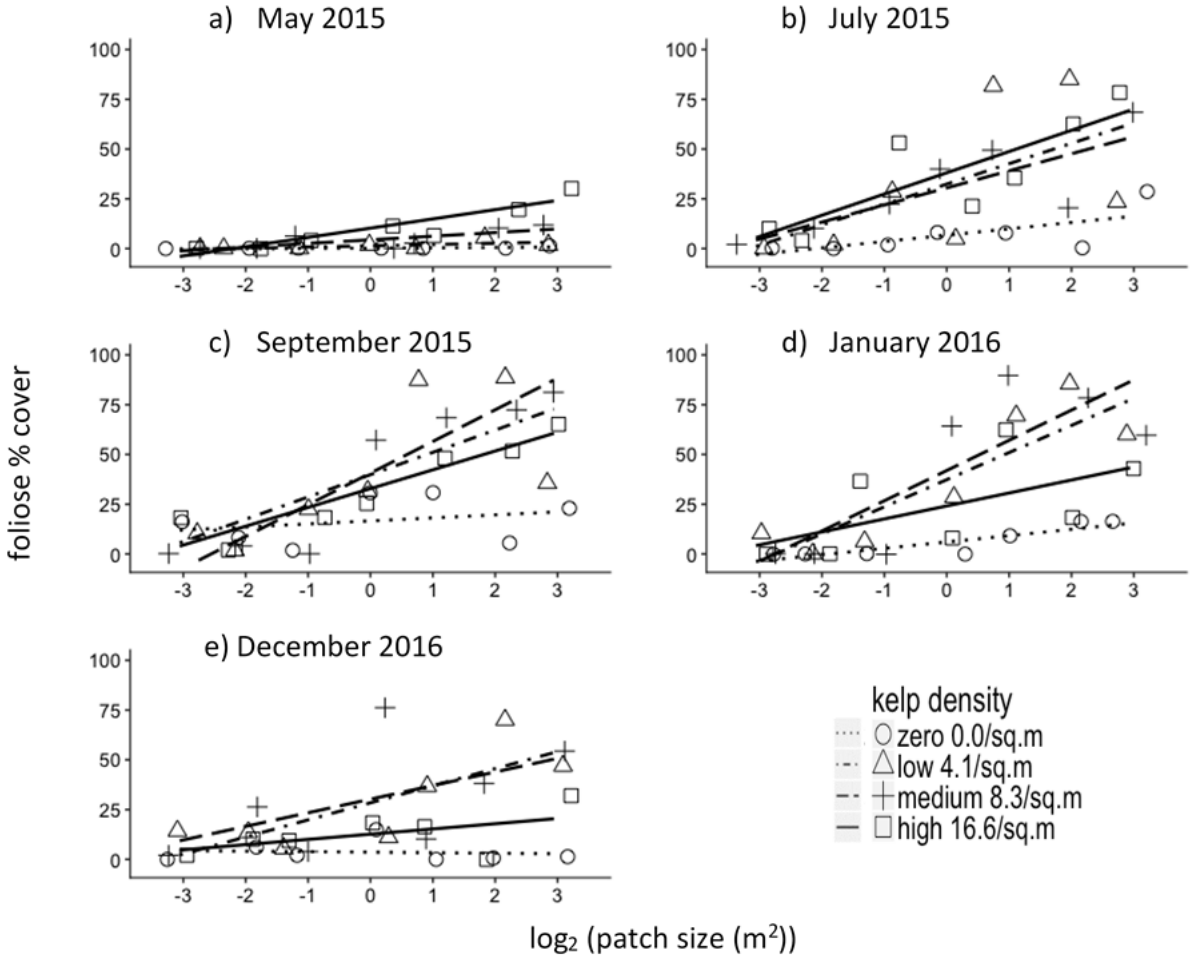


Figure 2.4. Percentage cover of foliose algae on the different patch size and kelp density on five sampling occasions (5, 7, 9, 13 and 24 months after installation of the reefs).

2.4.3 Effect of patch size and kelp density on algal biomass

Total algal biomass density (i.e. gm^{-2} not including kelp transplants) did not differ with patch size or kelp density, but significant effects were identified for different algal functional groups (Fig. 2.6, Table 2.4). The biomass of leathery macrophytes increased significantly with patch size and the biomass of branching corticated algae as well as filamentous algae

both showed a significant density x patch size interaction. Whilst the biomass of foliose algae differed with kelp density (zero < low).

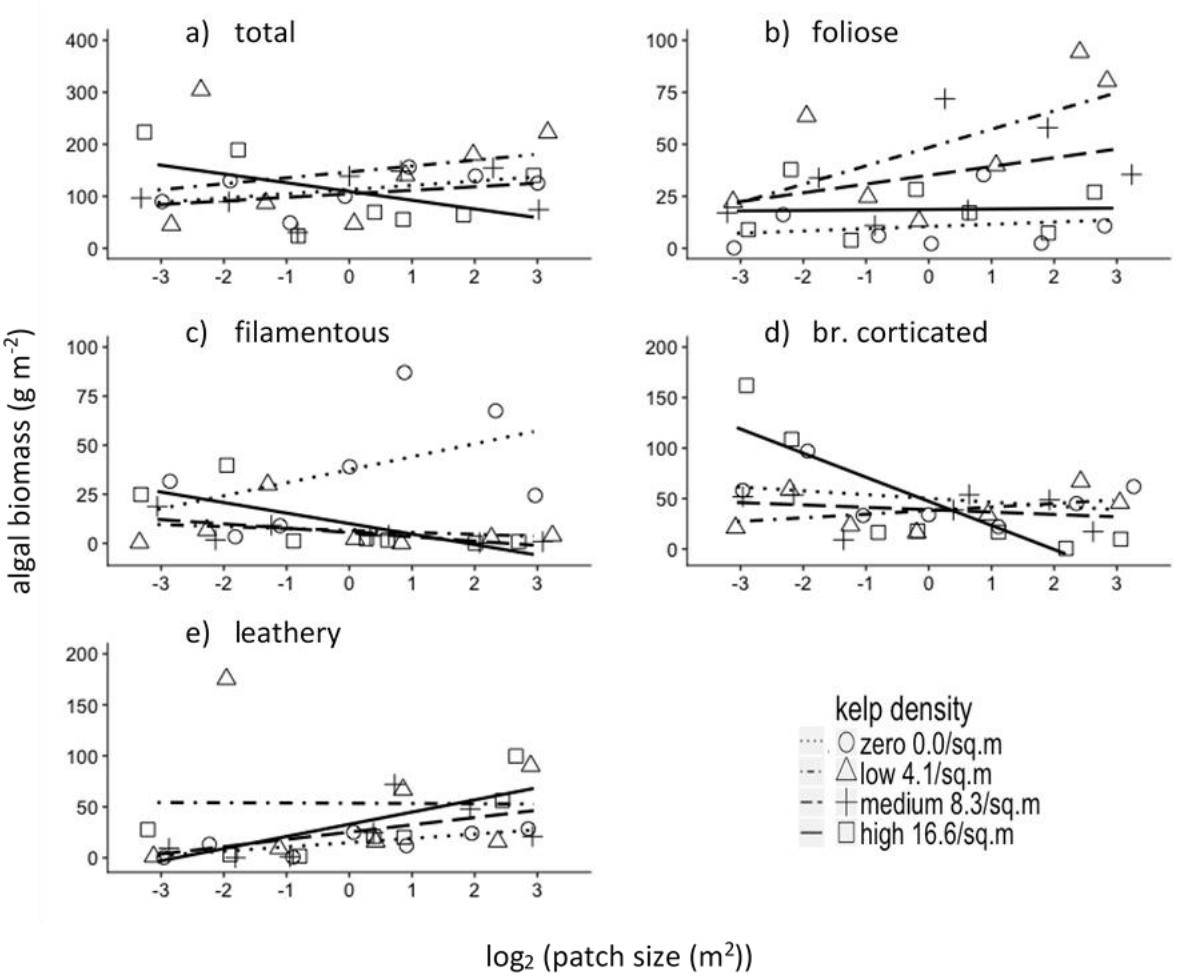


Figure 2.5. Biomass of different algal functional groups on the different patch size and kelp density at the end of the experiment (December 2016, after 24 months).

2.4.4 Effect of patch size and kelp density on sessile invertebrates

Patch size and kelp density interactively affected the total percentage cover of invertebrates, but invertebrate cover appeared to increase with patch size on reefs with kelp, whilst it remained constant across reefs of different size when kelp was absent (Figs. 2.5a, Table 2.2). Cover of invertebrates was approximately three times greater on the largest reefs with kelp compared to those without. The most abundant sessile invertebrate colonising the surface of reefs beneath the algae was the native oyster *Ostrea angasi* (Figs. 2.2d, 2.4c). On larger reefs with kelp, these oysters covered > 50 % and up to 75 % of the reef surface. Oyster cover increased significantly with patch size and differed with kelp density (no kelp < low and medium kelp density (Table 2.2)). Although not significantly different, reefs with intermediate kelp densities also supported a higher cover of oysters than reefs with high kelp densities. Ascidians and sponges were the next most abundant invertebrates, although their covers were typically < 20 %. Ascidians were more abundant on larger reefs and those supporting high kelp densities (vs. zero and low-density kelp), whilst sponges showed significantly greater cover on larger reef sizes.

model	factor	SS (df)	F-value	p-value	Post-hoc
ALGAL BIOMASS (g m^{-2})					
total $(x)^{0.41}$	kelp density	3.22 (3, 23)	0.36	0.781	
	log_2(patch size)	1.28 (1, 23)	0.43	0.517	
foliose $(x)^{0.35}$	kelp density	12.87 (3, 23)	6.44	**0.003 ***	zero < low = medium
	log_2(patch size)	2.39 (1, 23)	3.59	0.071	
filamentous $(x)^{0.16}$	kelp density* log_2(patch size)	0.81 (3, 20)	3.41	**0.037 ***	
filamentous (no zero density) $(x)^{0.13}$	kelp density	4.6e-03 (2, 17)	0.04	0.959	
	log_2(patch size)	0.38 (1, 17)	3.59	**0.018 ***	
br. corticated $(x)^{0.32}$	kelp density* log_2(patch size)	11.12 (3, 20)	6.10	**0.004 ***	
br. corticated (no high density) $(x)^{0.58}$	kelp density	9.17 (2, 17)	0.64	0.541	
	log_2(patch size)	0.44 (1, 17)	0.06	0.808	
leathery $(x)^{0.22}$	kelp density	0.99 (3, 23)	1.15	0.351	
	log_2(patch size)	3.61 (1, 23)	12.50	**0.002 ***	
INVERTEBRATE % COVER					
total $(x)^{1.77}$	kelp density* log_2(patch size)	1.8e06 (3, 20)	3.12	**0.049 ***	
total (no zero density) $(x)^{2.24}$	kelp density	3.7e07 (2, 17)	1.21	0.323	
	log_2(patch size)	6.8e08 (1, 17)	44.26	**<0.001 ***	
ascidian $(x)^{0.08}$	kelp density	0.56 (3, 23)	5.42	**0.006 ***	high > zero = low
	log_2(patch size)	0.26 (1, 23)	7.59	**0.011 ***	
sponge $(x)^{0.45}$	kelp density	3.08 (3, 23)	1.56	0.226	
	log_2(patch size)	10.43 (1, 23)	15.84	**< 0.001 ***	
oyster $(x)^{0.85}$	kelp density	941.49 (3, 23)	6.75	**0.002 ***	zero < low = medium
	log_2(patch size)	1163.40 (1, 23)	25.04	**< 0.001 ***	
ALGAE RICHNESS AND DIVERSITY					
richness $(x)^{0.41}$	kelp density	0.02 (3, 23)	1.02	0.401	
	log_2(patch size)	4.11 (1, 23)	62.29	**< 0.001 ***	
diversity $(x)^{-0.34}$	kelp density	1.8e-03 (3, 23)	0.58	0.633	
	log_2(patch size)	8.1e-03 (1, 23)	7.71	**0.011 ***	
INVERTEBRATE RICHNESS AND DIVERSITY					
richness $(x)^{0.85}$	kelp density	5.73 (3, 23)	2.40	0.094	
	log_2(patch size)	8.53 (1, 23)	10.70	**0.003 ***	
diversity $(x)^{0.91}$	kelp density	1.09 (3, 23)	6.06	**0.003 ***	high > low = medium
	log_2(patch size)	0.02 (1, 23)	0.26	0.617	

Table 2.2 Results of ANCOVA models testing the effects of kelp density and patch size on the biomass of different understory algal functional groups, the percentage cover of sessile invertebrate functional groups, as well as the richness and diversity of algal species and invertebrate functional groups, at the end of the experiment (December 2016). Model outputs are either from full models where there was a density x patch size interaction or unsaturated models after confirming homogeneity of slopes. Response variable transformations are shown in the model column. The covariate (patch size) was log_2 transformed. Significant p-values from the ANCOVA are bolded and denoted with *****. Significant post-hoc pairwise comparisons are indicated in the Post-hoc column.

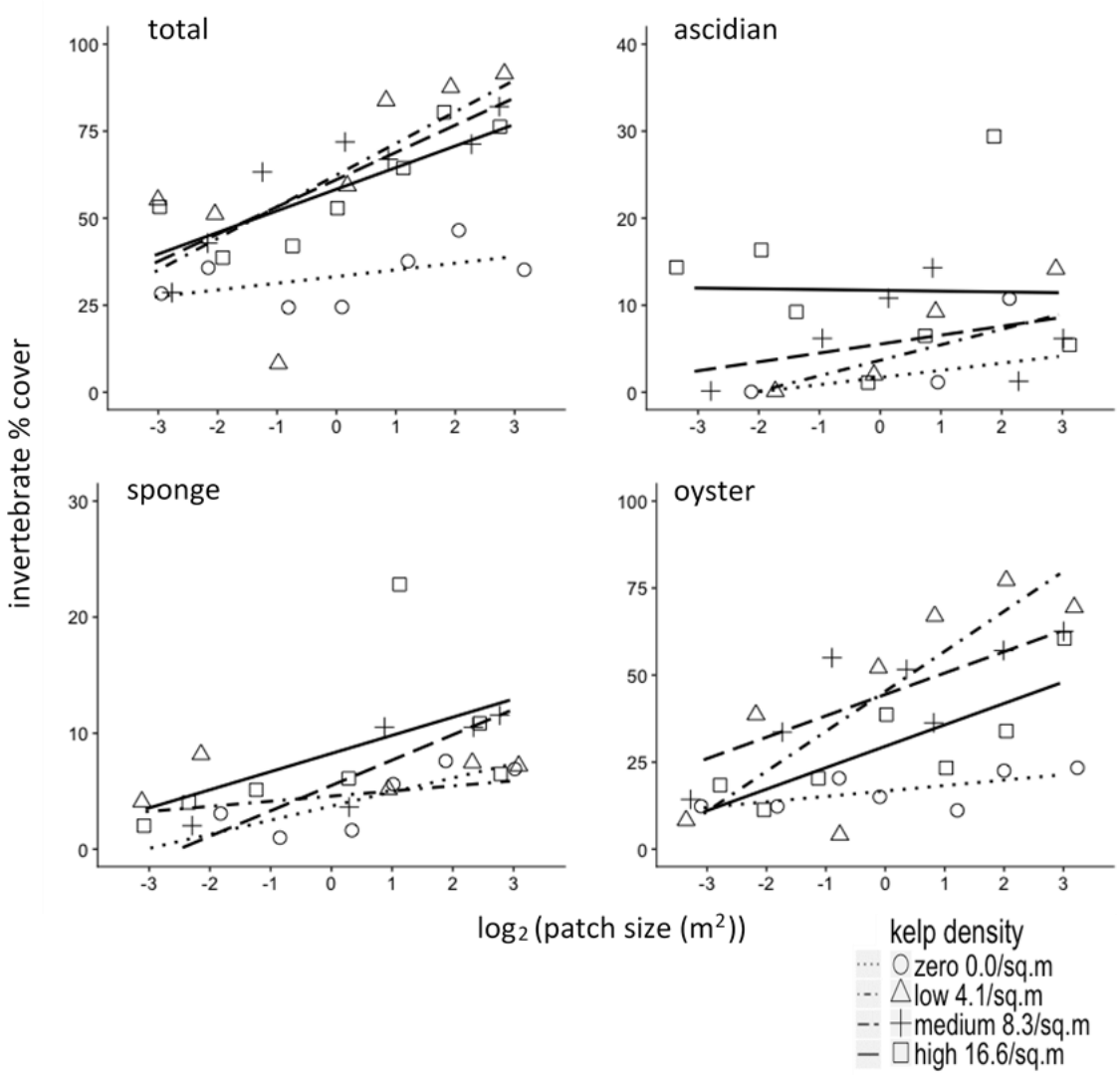


Figure 2.6. Percentage cover of dominant invertebrate groups on reefs of different patch size and kelp density at the end of the experiment (December 2016, after 24 months) following removal of understory algae.

2.4.5 Effects of kelp patch size and density on species richness and diversity of algae and invertebrates

Unsurprisingly total richness of algae and invertebrates increased significantly with patch siz e (due to the dif*f*erent areas being sampled) but were not affected by kelp density (Fig. 2.7, Table 2). Only algal diversity increased significantly with patch size, whilst only the diversity of invertebrates was significantly affected by kelp density (high > low = medium).

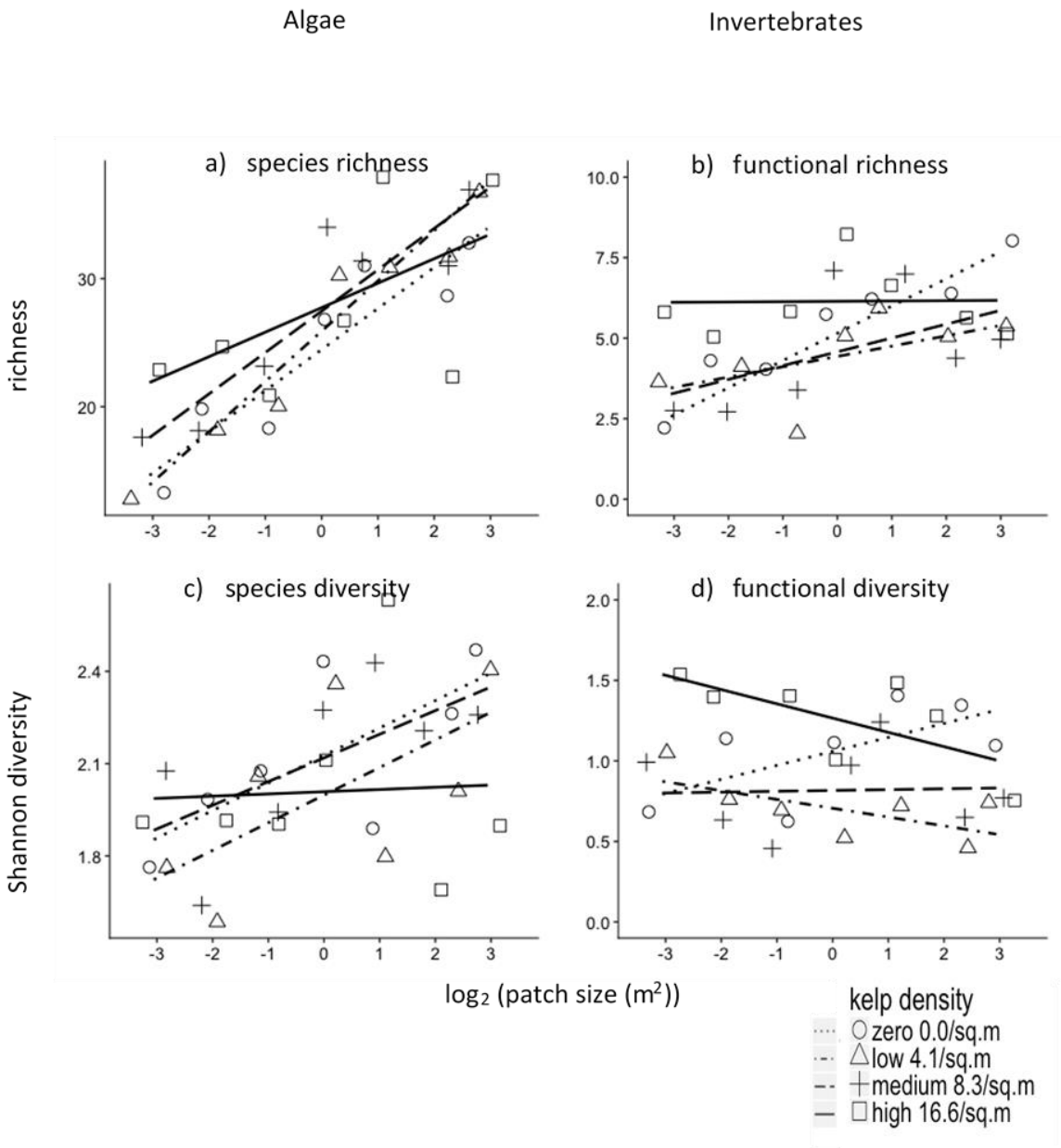
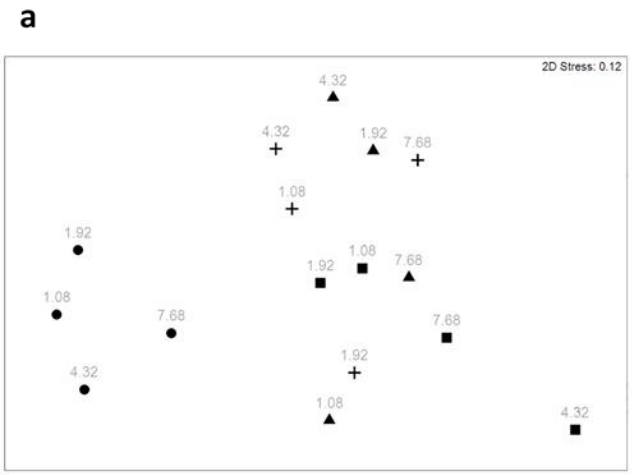


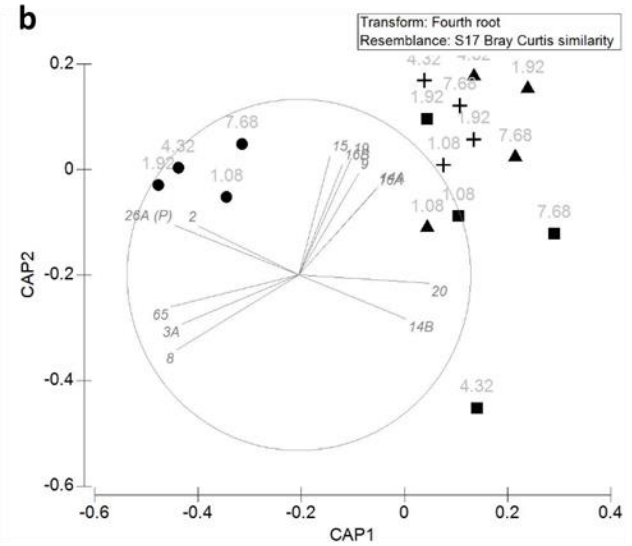
Figure 2.7. Richness and Shannon diversity of algal and sessile invertebrates on reefs of different patch size and kelp density at the end of the experiment (December 2016).

2.4.6 Effect of kelp density on the community structure of understory algae and sessile invertebrates

The MDS, CAP and PERMANOVA for the community structure of algae and invertebrates (Fig. 2.8, 2.9) indicated that there were differences between reefs with and without kelp, although the pairwise comparisons in the PERMANOVA were nearly always marginally

non-significant (except for understorey algae, where the comparison across reefs with no kelp vs. kelp at high density was significant) (Table. 3). The algal communities on reefs without kelp tended to be defined largely by filamentous and branching corticated growth forms along with the leathery brown species *Dictyopteris muelleiri* (Fig. 2.8). In comparison, reefs with intermediate kelp densities were defined predominantly by species with foliose growth forms (e.g. *Hemineura frondosa* and *Ulva* sp.), while on reefs with a high kelp density understory algae tended to be dominated by larger corticated species such as *Pollexfenia lobata* and the leathery macrophyte *Sargassum vestium* (Fig. 2.8). For the invertebrates, reefs without kelp could be distinguished from those with kelp by their low cover of oysters and colonial ascidians and higher prevalence of mussels, barnacles and bryozoans (Fig. 2.9). Algal and invertebrate communities both showed non-significant differences in dispersion across kelp density (algae: $F = 2.76$, $P = 0.09$; invertebrates: $F = 2.33$; $P = 0.13$).





ID	species name	ID	species name
2	*Dictyopteris muelleiri*	15	*Sarcodia marginate*
3A	*Filamentous green 1.*	16A	*Callophyllis rangiferina*
6	*Corticated red 1.*	16B	*Plocamium augustum*
8	*Filamentous red 1.*	20	*Pollexfenia lobata*
9	*Cladostepanus spongiosus*	26A	*Gracilaria Secundata*
14A	*Hemineura frondosa*	65	*Unknown brown 1.*
14B	*Gliocladia polycarpa*		

Figure 2.8. MDS (a) and CAP (b) of understory algal community structure (based on dry weight from destructive sampling) on reefs with different kelp densities. Vector overlay in CAP depicts species with Spearman correlations > 0.5. Reef size is shown in grey text.

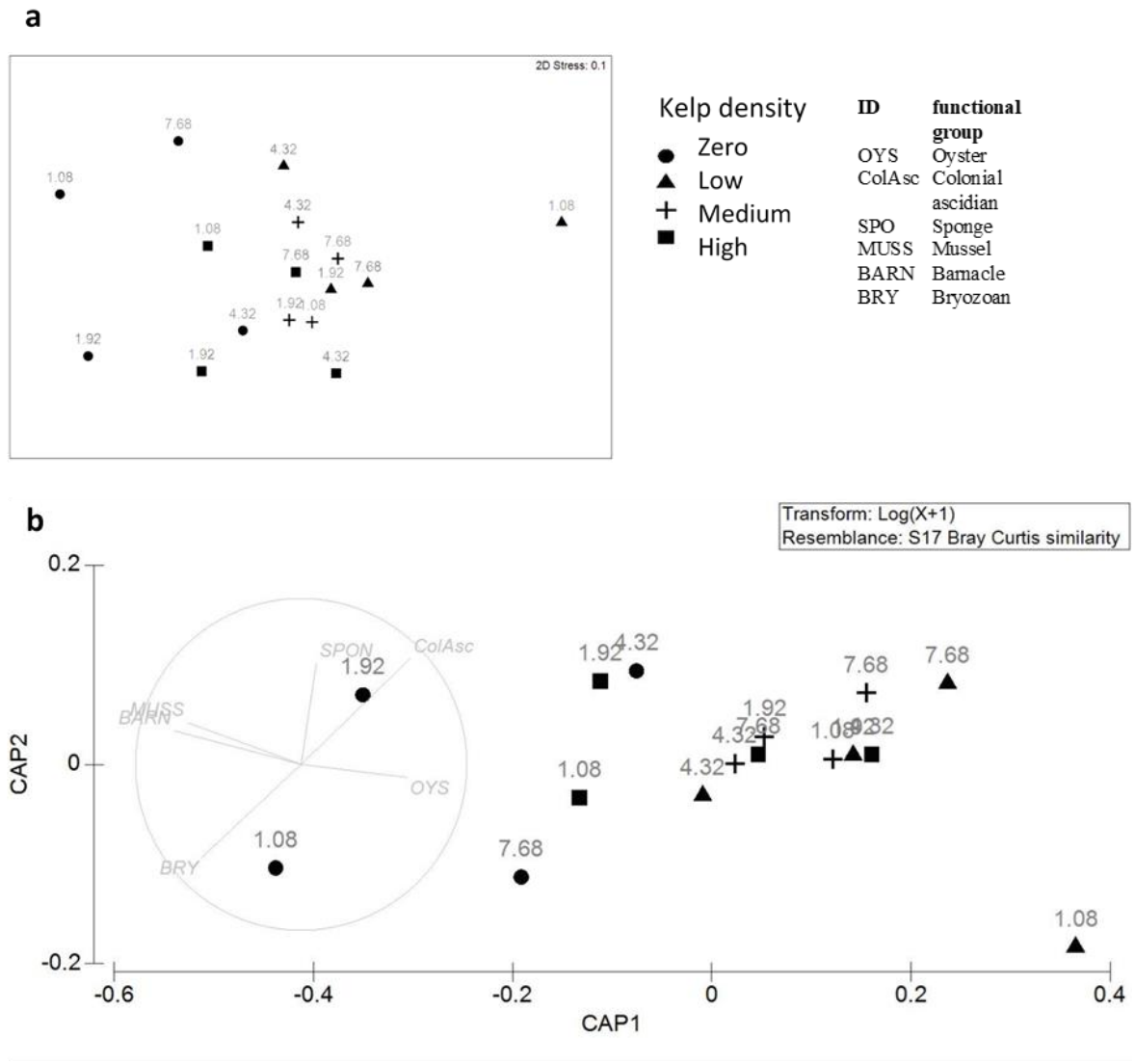


Figure 2.9 a) MDS and b) CAP of sessile invertebrate community structure determined from photo quadrats taken following destructive sampling of the macroalgae at the end of the experiment. Vector overlay in CAP depicts functional groups with Spearman correlations > 0.6. Reef size is shown in grey text.

2.4.7 Effect of abiotic and biotic factors on turfs

The best biotic predictor variable(s) explaining turf cover was foliose algal cover (-'ve (negative association); $r^2 = 0.75$). This model had slightly better predictive power than the best abiotic model, for which light (+'ve (positive association); $r^2 = 0.71$) was the only predictor variable (AIC = 232.20 vs. 235.61). The best model combining biotic and abiotic factors included light, sediment deposition (non-significant (NS)) and the percentage cover of

foliose algae and explained 86 % of variability in turf cover (AIC = 217.7; Table 4). Hierarchical partitioning of the biotic and abiotic factors showed that both light and foliose algal cover made similar significant independent contributions (34 % vs. 44 % respectively).

2.4.8 Effect of abiotic and biotic factors on foliose algae

Turf cover was the best biotic predictor variable for foliose algal cover (-'ve; r^2 = 75 (vs. sessile invertebrates: r^2 = 0.55)), which exceeded the predictive performance of light (-'ve) as the best abiotic predictor (AIC = 93.85 vs. 111.80). This was barely improved upon through combining biotic and abiotic variables in a single model, which selected turf percentage cover and sediment deposition (AIC = 91.35) (Table 4). The hierarchical partitioning of biotic and abiotic factors showed that only turf cover had a significant independent contribution (of 83 %).

2.4.9 Effect of abiotic and biotic factors on sessile invertebrates

The optimal model relating cover of sessile invertebrates with other variables identified light (-'ve) and sediment deposition (+'ve) as key abiotic predictors (AIC = 189.36, r^2 = 0.84), but only light had a significant independent effect (44.4 %). Turf cover (-'ve) was also a reasonably good predictor of sessile invertebrate cover (r^2 = 0.65), but needed to be dropped in the combined model due to its high correlation with light.

2.4.10 Effect of abiotic and biotic factors on E. radiata recruitment

The optimal model for the density of *E. radiata* recruits was the abiotic model which included light (-'ve) and water flow (+'ve; AIC = 33.19, r^2 = 0.95), but only light had a significant independent effect (47.4 %). This model however, was only a slight improvement

on the simpler model using only the single predictor variable of kelp number (+'ve; AIC = 35.90, $r^2 = 0.93$).

2.5 Discussion

Complete absence of kelp and decreasing patch size resulted in increased cover of turf algae, whilst sessile invertebrates and foliose algae decreased in abundance with reductions in patch size and foliose algae was most dominant with low and medium densities of kelp. The influence of kelp structure on the availability of light at the benthos and cover of turf algae appeared to be the most important factors shaping understory assemblages. Spore production and/or abiotic ecosystem engineering by adult kelp (largely through the reduction in benthic light levels), not understory algae, appeared to be the most important factor(s) driving the abundance of macroscopic *E. radiata* recruits on the reefs. Although it is possible that results from destructive sampling were confounded by differences in edge:area of samples from reefs < $1.08m^2$ vs. reefs ≥ $1.08m^2$, these results were highly consistent with what was observed in the photo-quadrats, which did not have this potential confound. Even though the assemblages which established on the artificial reefs are likely to differ from the communities on natural reef experiencing varying degrees of kelp loss (due to the artificial substratum and differences in the surrounding environmental conditions), we believe that the influences of kelp structure and ecosystem engineering on key functional groups that we identified are likely to play out on rocky reef ecosystems experiencing change. There are additionally implications for the restoration of *E. radiata* in coastal areas, where it is likely that the development of benthic communities can be influenced by varying the structure of the adult kelp.

2.5.1 Drivers of turf algal abundance

Our results support the notion that increased sub-canopy light levels associated with degradation of kelp habitat is a major factor leading to increased dominance of turf algae (Connell 2005). However, most reefs > 1.08 m^2 that supported kelp had sufficiently low light levels (< 200 µmol m^{-2} s^{-1}) (Layton et al. 2019b) to restrict turf cover to < 30 % of reef surface area, indicating that even relatively degraded kelp forests are effective in suppressing turfs. Turfs may become more dominant after substantial kelp loss due to their ability to cope with – and indeed thrive on – high light levels, which can inhibit other algal species (Copertino et al. 2006). Additionally, results also indicate that foliose algae have a strong negative relationship with cover of turfs. Given the sequence in which turf algae and foliose algae established on the reefs and reached an apparent equilibrium (turfs first then foliose algae), it is likely that decreasing kelp patch size and density led to increased turf cover (due to increased benthic light), and in turn this limited the cover of foliose algae. Thus, kelp may facilitate the establishment of relatively slow-to-establish foliose species, through competitive release from turfs (Benes and Carpenter 2015). Once established, it is unclear whether foliose algae are able to resist subsequent turf incursions if kelp is lost.

2.5.2 Drivers of foliose algae abundance

In contrast to turfs, absence of kelp and reductions in patch size are likely to cause declines in foliose algal cover, however, reductions in kelp density could have a positive effect on foliose algae. Although not supported by any post-hoc pairwise comparisons, reefs with medium and low kelp densities had greater cover of foliose algae than reefs with high kelp densities for the last three sampling times (September 2015 and January and December 2016 (Fig. 2.3)), and this was supported by biomass results (Fig. 2.6). Additionally, Flukes et al. (2014) also observed elevated foliose algal cover in response to reductions in *E. radiata* density on

natural rocky reef. This indicates that the nature of kelp loss (complete vs. reduction in density) could have important implications for the associated assemblages. Both light and turf cover were strongly (negatively) associated with foliose algae (Table 4), but these predictors where highly correlated and could not be combined in a single multiple regression model. The separate analyses of biotic and abiotic factors showed that turf cover was the better predictor (than light) of foliose algal cover. This is consistent with the idea that light is a strong driver of turf cover, which then limits the cover of foliose algae, however, there may also be less important direct effects of light on foliose algae. Turfs are likely to manifest a range of physical and chemical stressors (e.g. chemical boundary layer effects, high siltation, increased exposure to grazing etc.), which help them to outcompete other algal species (Airoldi 1998, Larkum et al. 2003, Short et al. 2015, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Layton et al. 2019a). High light can be an important driver of foliose algae on its own, having either positive effects (Wernberg et al. 2005) or negative effects on species acclimated to low light levels (Toohey et al. 2004). We suspect that the high cover of foliose algae on reefs with intermediate kelp densities resulted mainly from the combined effects of turfs impeding foliose algae on reefs with no kelp, and a lack of light impeding their establishment on reefs supporting high densities of kelp. Our results also indicate that a decline in sediment deposition associated with loss of kelp patch size and density, has a positive yet minor effect on foliose algae, although the potential mechanism by which sediment deposition effects foliose algae is unclear.

		Model optimisation procedure		Hierarchical partitioning	
Nature of predictor variables	**Selected predictor variables**	**Adj. r^2**	**AIC**	**Included predictor variables**	**Independent contribution (%)**
TURF % COVER					
Abiotic	Light	0.71	235.61	Deposition Accumulation Flow Light	13.86 16.19 * 2.71 67.24 *
Biotic	Foliose (Sqrt)	0.75	232.20		
Abiotic & biotic	Light Foliose Deposition (NS)	0.86	217.70	Foliose Light Deposition Accumulation Flow	43.64 * 34.40 * 9.90 10.36 1.70
FOLIOSE % COVER (sqrt)					
Abiotic	Light	0.52	111.83	Light Deposition Accumulation Flow	77.01 * 6.11 12.21 4.68
Biotic	Turf	0.75	93.85		
Abiotic & biotic	Turf Deposition	0.77	91.35	Turf Deposition Accumulation Flow	82.88 * 5.27 8.66 3.19
SESSILE INVERTEBRATE % COVER					
Abiotic	Light Deposition	0.84	189.36	Light Deposition Accumulation Flow	70.40 * 8.85 15.28 5.46
Biotic	Turf	0.65	208.25		
Abiotic & biotic	*Same as abiotic*			Light Deposition Flow Accumulation Foliose (sqrt)	44.40 * 6.68 3.96 11.21 33.74 *
***ECKLONIA* RECRUIT DENSITY**					
Abiotic	Light Flow	0.95	33.19	Light Deposition Accumulation Flow	47.37 * 24.29 12.54 15.80
Biotic	Turf (sqrt)	0.44	55.44		
Abiotic & biotic	*Same as abiotic*			Light Deposition Accumulation Flow Foliose (sqrt)	45.68 * 22.81 12.16 15.87 3.49
Kelp number	Kelp number (log_{10})	0.94	35.90		

Table 2.3. Summary of multiple regression analyses testing abiotic, biotic and a combination of biotic and abiotic predictor variables on turf algae, foliose algae and sessile invertebrate percentage cover as well as the density of visible *E. radiata* recruits. The Nature of predictor variables column shows whether the predictor variables considered in the model were abiotic, biotic or both. Highly correlated terms that contributed less to the explained variability than the term they were correlated with were dropped from the analysis and noted in brackets. Terms initially selected by the model optimization procedure are shown under the selected predictor variables column and non-significant terms are denoted with NS. The performance of the optimised model is shown in terms of the adjusted r^2 values and Akaike's Information Criterion. Results of the hierarchical partitioning are presented in terms of the independent contribution of each predictor variable to the explained variance in the response variable. Significant contributions are denoted with *.

2.5.3 Drivers of sessile invertebrate cover

Similar to foliose algae, absence of kelp and reductions in patch size negatively impacted sessile invertebrates. Cover of invertebrates was more strongly (negatively) correlated with abiotic factors including light and sediment deposition compared to understory algal cover. However, the reasonably strong negative relationship between turfs and invertebrates (r^2 = 0.67) indicates that understory algae may also have a role in influencing invertebrate cover, however, this could not be explored in combination with light (due to co-linearity). The strong effect of abiotic factors on benthic invertebrates is consistent with findings by Duggins et al. (1990), which similarly found negative effects of light and sediment deposition, and little direct effect of flow on the recruitment of a variety of sessile invertebrate species. In our study however, the independent contribution of sediment deposition was minor and not significant. Potentially, the combination of high light and sediment deposition may provide poor cues for settlement of invertebrate larvae and/or illicit increased mortality of newly settled recruits (Young and Chia 1984). Increased post-settlement mortality might also arise from increased competition for space with algae, which are more prevalent under high light (Miller and Etter 2008). Relatively little is known about the recruitment preferences of *Ostrea angasi*, the dominant invertebrate species across the reefs, however, the closely related oyster species *O. edulis* is negatively photo-tactic (Bayne 1969), which is consistent with our results.

2.5.4 Primary Production of the understory

Reduced cover of canopy-forming kelp which affects the composition of understory algae and increases sub-canopy light is likely to impact primary production of the understory community (Richards et al. 2011, White and Shurin 2011, Pedersen et al. 2014). A transition towards foliose species, which may occur with declines in kelp density, could reduce

biomass-specific primary productivity as foliose algae tend to be less productive (relative to biomass) compared to filamentous and branching algae (Miller et al. 2009). Additionally, increased abundance of foliose algae may also cause increased shading of lower growing species, further reducing primary production (Binzer et al. 2006). However, area-specific declines in productivity may not occur with increases in foliose algae as foliose species tend to have a greater biomass density than other filamentous growth forms (Miller et al. 2009) and multi-layered algal communities have been shown to outperform more simple structures (Alestra et al. 2014). In contrast, a transition towards a turf dominated understory, which is likely to result from large scale kelp loss, could increase productivity per unit of algal biomass but reduce area-specific productivity (Miller et al. 2009). Changes in the composition of understory species and levels primary production may have profound consequences for costal food webs, especially if there an associated shift in the productivity of small grazing invertebrates colonising the understory (i.e. secondary productivity) as these organisms provide a critical trophic link for higher order consumers, especially fishes (Edgar and Aoki 1993, Edgar and Shaw 1995a).

2.5.5 E. radiata recruitment

The positive influence of *E. radiata* patch size and density on recruitment to our artificial reefs was previously identified in Layton et al. (2019b). Here, we build on these findings by demonstrating a strong negative relationship ($r^2 = 0.95$) between abiotic factors (mainly light) and the density of recruits, which supports the notion that adult kelp facilitate their own population replenishment through abiotic ecosystem engineering (Layton et al. 2019b). However, we also found an equally strong relationship between the number of adult kelp of the reef and recruit density ($r^2 = 0.93$), which is also consistent with the alternative hypothesis that the density of recruits is limited by spore production and thus determined by the local

population of adults. We did not investigate either influence further, however, it is clear that more adult kelp led to greater observed recruitment (log relationship). In contrast to our prediction and other studies (Kennelly 1987a, Tatsumi and Wright 2016), we found that understory algae were unlikely to have been an important driver of recruitment (on reefs where natural recruits were observed).

Consistent with the negative relationship between light and recruitment that we observed, high light levels can cause photo-inhibition and tissue necrosis of *E. radiata* juveniles (Wood 1987) and have detrimental effects on juvenile survivorship (Tatsumi and Wright 2016). High water flow which has the capacity to dislodge microscopic and macroscopic juveniles, has additionally been shown to negatively influence on recruitment (Eckman et al. 1989), however, we didn't observe a significant relationship between recruitment and flow.

Although not observed in this study, both turfs and foliose understory algae can have detrimental impacts on kelp recruitment (Kennelly 1987a, Tatsumi and Wright 2016). This may occur through a number of mechanisms including shading (Tatsumi and Wright 2016), competition for space (Airoldi 1998) and retention of sediment by turfs (Isæus et al. 2004). The fact that the understory algae appeared to have a negligible effect on recruitment, suggests that algae which detrimentally impact recruitment, were either not present in sufficient quantities to have a major impact on recruitment or that other factors overshadowed their effect. Because we didn't observe any recruitment on reefs ≤ 0.48 m^2 and on reefs without transplanted kelp, we are unable to elucidate whether understory algae impacted recruitment on reefs nearly and completely devoid of kelp. Layton et al. (2019b) found zero survivorship of out-planted microscopic and macroscopic juveniles on this subset of reefs, which indicates very strong recruitment inhibition under situations where kelp are practically

absent. Although, it is unknown whether understory algae contributed to this inhibition in any way.

In relatively pristine *E. radiata* forests of a sufficiently large size, the density of adults and therefore potential zoospore supply, tends not to reflect or limit recruit numbers (Wernberg 2009), even though greater zoospore concentrations may lead to improved settlement success (Tatsumi and Wright 2016). In-tact forests tend to have an abundant supply of dormant microscopic propagules (Edwards 2000), but limited light levels at the benthos to support their growth and development (Toohey and Kendrick 2007). Consequently, the loss of adults, which leads to elevated benthic light levels, tends to be associated with a pulse in recruitment and a negative relationship between the number of adult kelp and the abundance of macroscopic recruits (Johnson and Mann 1988, Kennelly and Underwood 1993, Flukes et al. 2014). The strong positive relationship that we observed (between the density of visible recruits and abundance of adults), indicates that different processes are likely to have limited recruitment to our reefs. Spore production was probably a more important driver of recruitment than access to benthic light. Potentially, this situation may occur with recruitment at smaller spatial scales, in situations where kelp patches are reproductively isolated, or in areas without recent cover of kelp (and therefore no 'seedbank' of juveniles). Consequently, addressing spore limitation is likely to a key consideration in the restoration/establishment of new kelp forest ecosystems.

Differences in the structure of canopy-forming kelp on rocky reefs will both directly (through benthic light) and indirectly (through proliferation of turfs) influence the understory assemblages. Small patch sizes and absence of kelp are likely to create conditions which favour dominance of turfs, whilst larger patches and intermediate densities of kelp are likely

to create more favourable conditions for foliose species. Although differences in the structure of adult kelp may affect recruitment and the stability of kelp ecosystems, the importance of recruitment inhibition by understory algae is likely to be context specific.

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Chapter 3. Ecosystem engineering by a canopy-forming kelp facilitates recruitment of native oysters

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3.1 Abstract

Ecosystem engineers are species that influence the abiotic and biotic environment around them and may assist the restoration of associated species, including other habitat-forming species. We deployed an array of 28 artificial reefs with transplanted *Ecklonia radiata*, the dominant canopy-forming kelp species across southern Australia, to investigate how the patch size and density of *E. radiata* influenced the establishment of the associated communities of plants and animals. Many of the reefs were rapidly colonised by *Ostrea angasi*, a critically depleted reef-forming oyster. Over the 24-month deployment of the reefs, thick oyster mats formed across the entire surface of many of the reefs with estimated biomass densities exceeding 5 kg of live oysters/m^2, however oyster density was dependent on *E. radiata* patch size and density. Increasing patch size and the presence of kelp resulted in significantly higher densities of oysters five months after the reefs were deployed and at the end of the experiment, where oysters were approximately three times more numerous on reefs with kelp compared to those without kelp. *E. radiata* appeared to facilitate the establishment of *O. angasi* largely through its capacity to reduce benthic light and thus suppress competition from turfing algae. These results may inform the development of novel approaches to tackle recruitment bottlenecks affecting the restoration of *O. angasi* reefs.

KEY WORDS: facilitation; kelp; *Ostrea angasi*; recruitment; shellfish reef; turf algae

3.2 Conceptual implications

• Facilitation whereby the presence of one species supports the occurrence of another should receive careful consideration in the design of restoration projects in the marine environment.

• There may be a beneficial association between kelp and oysters that has not described previously in the literature which could have been obscured by over exploitation of oysters and habitat degradation that occurred prior to scientific descriptions of these ecosystems.
• Competition from algal turfs could represent a significant barrier to restoration in marine systems; however, could be mitigated through providing the mechanism by which kelp and other species suppress turfs.

3.3 Introduction

Facilitation often plays a major role in influencing community establishment and ecological processes (Bruno et al. 2003). Species that facilitate the establishment of communities are likely to provide key functions that may assist the restoration of other species. Positive interactions have been incorporated into the practice of terrestrial ecological restoration through the use of *nurse* plantings, which are used to enhance the establishment of vegetation (Padilla and Pugnaire 2006). Typically this involves planting robust pioneer shrub species which modify the surrounding environmental conditions and improve the survival prospects of closely associated seedlings (e.g. by increasing water and nutrient availability, and providing protecting against grazers) (Filazzola and Lortie 2014). However, there are limited examples of this practice in marine environments, despite the presence of influential canopy-formers which provide a range of facilitatory functions in marine ecosystems (Halpern et al. 2007, Bulleri 2009, Silliman et al. 2015).

Similar to the trees and shrubs in terrestrial systems, large canopy-forming brown macroalgae (hereafter referred to as *kelp*) are ecosystem engineers that facilitate the establishment of associated communities through the provision of habitat structure and by modifying the local

environmental conditions including the abundance of other influential species (Teagle et al. 2017, Layton et al. 2019b). Kelps have a particularly strong effect on the abiotic environment beneath their canopy, including their influence on light availability, sedimentation (deposition and accumulation), water flow and scour (Eckman et al. 1989, Kennelly 1989, Wernberg et al. 2005, Layton et al. 2019b). These abiotic conditions then shape the composition of understory algal and sessile invertebrate assemblages (Kennelly 1987c, 1989, Duggins et al. 1990, Wernberg et al. 2005, Flukes et al. 2014), which are likely to further influence other species (Arkema et al. 2009). Kelp structure also affects the abundance of macroinvertebrates and fishes, which can impact trophic interactions (Anderson and Millar 2004) and may exert top-down influences on community establishment (Virnstein 1977). While kelp forests are important ecosystems in their own right, their role as ecosystem engineers that modify abiotic and biotic factors may also provide a tool to assist the restoration of other important habitat-forming species.

The structure of kelp stands, in terms of the size of patches and the density of adults has a significant effect on the sub-canopy abiotic and biotic environment. Reductions in patch size and adult density results in an increase in benthic light, sediment accumulation and water flow, whilst sediment deposition is likely to decrease (Wernberg et al. 2005, Layton et al. 2019b). Kelp also scour the benthos with their laminae in surge (Kennelly 1989), although the effect of kelp structure on scour are unclear. Critical to the development of robust and diverse benthic communities, kelp can suppress the development of low-growing filamentous algal turfs through canopy shading, sediment removal, and damage to small understory algae by scour (Kennelly 1989, Connell 2005, Reeves et al. 2018). Turfs can stifle the establishment of other benthic species through competition for space, via their tendency to trap sediments and possibly by forming a distinct chemical boundary layer (Connell et al.

2014, O'Brien and Scheibling 2018, Reeves et al. 2018, Layton et al. 2019a). Thus, the recruitment and establishment of species beneath a kelp canopy is influenced by multiple abiotic and biotic factors, which vary with the structure of the kelp.

Oysters form three-dimensional structures on coastal reefs and have significant social, economic and ecological importance (Brumbaugh and Coen 2009, Zacherl et al. 2015, Gillies et al. 2018). They assist in shoreline stabilisation (Meyer et al. 1997), provide crucial habitat for fish and invertebrates (Grabowski et al. 2005), improve water quality (Grizzle et al. 2008, La Peyre et al. 2014) and support long-standing and economically valuable fisheries (MacKenzie 1996). However, over-extraction and increasing coastal degradation has caused the loss of around 85% of oyster reefs globally (Beck et al. 2011). In Australia, a massive decline of *Ostrea angasi* dominated reef ecosystems has occurred, with less than 1% of historically (commercially) harvested *O. angasi* reef systems remaining (Alleway and Connell 2015, Gillies et al. 2018). To redress the demise of this previously wide-spread ecosystem, several coordinated restoration efforts are currently underway (Gillies et al. 2017). These efforts follow from successful *Crassotrea virginica* oyster reef restoration projects in the United States (Schulte et al. 2009).

Establishing self-sustaining oyster populations is critical to the success of restoration projects. The recruitment of sessile species with a planktonic larval phase, such as oysters, depends on successful settlement and early post-settlement survival (Caddy and Stamatopoulos 1990). Indeed, the major obstacles that have been identified in the re-establishment of *O. angasi* reefs include a lack of suitable substratum for larval settlement, a depleted natural supply of larvae, as well as siltation, disease, and predation affecting vulnerable newly-settled recruits (Gillies et al. 2017). Many of these challenges can be partly addressed through the provision

of an artificial stable substratum (such as shell cultch or limestone) for oyster larvae to attach to, by supplementing natural recruitment with hatchery reared spat, and by constructing barriers to deter predators (Gillies et al. 2017). Nonetheless, achieving self-sustaining levels of natural recruitment across site locations which are exposed to different stressors, may require additional intervention options.

Because kelp structure affects multiple abiotic and biotic factors which can affect benthic recruitment, kelp presence and structure may have important ramifications for the settlement and subsequent survival of *O. angasi*. Little is known about the processes that affect the recruitment of *O. angasi*, however, high light, high silt accumulation, and lack of hard substratum have been shown to negatively influence the settlement of *Ostrea edulis* in Europe (Bayne 1969, Bromley et al. 2016, Smyth et al. 2017). This indicates that kelp presence which provides shading, removes sediment through benthic sweeping by laminae, and controls the colonisation of the understory by algae and invertebrates, could have a beneficial effect on *O. angasi* recruitment and therefore on restoration of oyster reefs. Furthermore, as these factors are likely to change with kelp patch size and density, different configurations of kelp are likely to modify any beneficial effect.

In order to determine the effect of different kelp structures (i.e. kelp patch size and density) on the recruitment and subsequent persistence of *O. angasi*, we monitored the density of naturally recruiting oysters across an array of artificial reefs of different sizes supporting various densities of Australia's most widespread kelp species, *Ecklonia radiata* at 5 and 24 months after the reefs were deployed. We also explored the relationship between the density of *O. angasi* that recruited to the reefs and abiotic factors (light, water flow, sediment

deposition and accumulation) and biotic factors (the percentage cover sessile species and the abundance mobile macroinvertebrates and fishes) influenced by the structure of *E. radiata*.

3.4 Methods

3.4.1 Experimental reefs

This research utilised the same array of 28 experimental reefs (hereafter 'reefs') with transplanted kelp (*Ecklonia radiata*) located off the west coast of Maria Island in eastern Tasmania, Australia, described in Layton et al. (2019b). Briefly, the reefs were positioned > 1.5km from the nearest natural rocky reef on a flat sandy substratum of uniform depth (6.5 m). The reefs were arranged in a square grid and were separated from one another by 25 m. The overall design was an analysis of covariance, with seven different patch sizes (0.12, 0.24, 0.48, 1.08, 1.92, 4.32 and 7.68 m^2) fully crossed with four kelp densities (0, 4.1, 8.3 and 16.6 kelp/m^2). Reefs of different patch sizes were constructed of varying numbers of concrete Turfstone pavers (Fig. 3.1a) elevated 300 mm above the substratum on a steel frame. The different kelp density treatments (hereafter referred to as: 'zero', 'low', 'medium' and 'high' densities), represented the mean density of *E. radiata* on natural reefs in eastern and southern Tasmania (medium), half that density (low), twice that density (high) and no kelp (zero) as controls for background recruitment levels. *E. radiata* was transplanted to the reefs (at the different densities) by collecting it from a nearby kelp forest and attaching it to the reefs by securing the holdfasts to the pavers with thick rubber bands and epoxy glue (Fig. 3.1b). The infrastructure was deployed in December 2014 and kelp was first transplanted to the reefs in January/February 2015. Experiments took place over two years (until December 2016) and during this time, constant kelp densities were maintained in the different treatments by replacing any lost or substantially degraded transplants with fresh adult kelp at regular

intervals (approximately every six weeks). Ecological communities were allowed to establish naturally on the reefs (Fig. 3.1c shows a completed reef, one year after deployment).

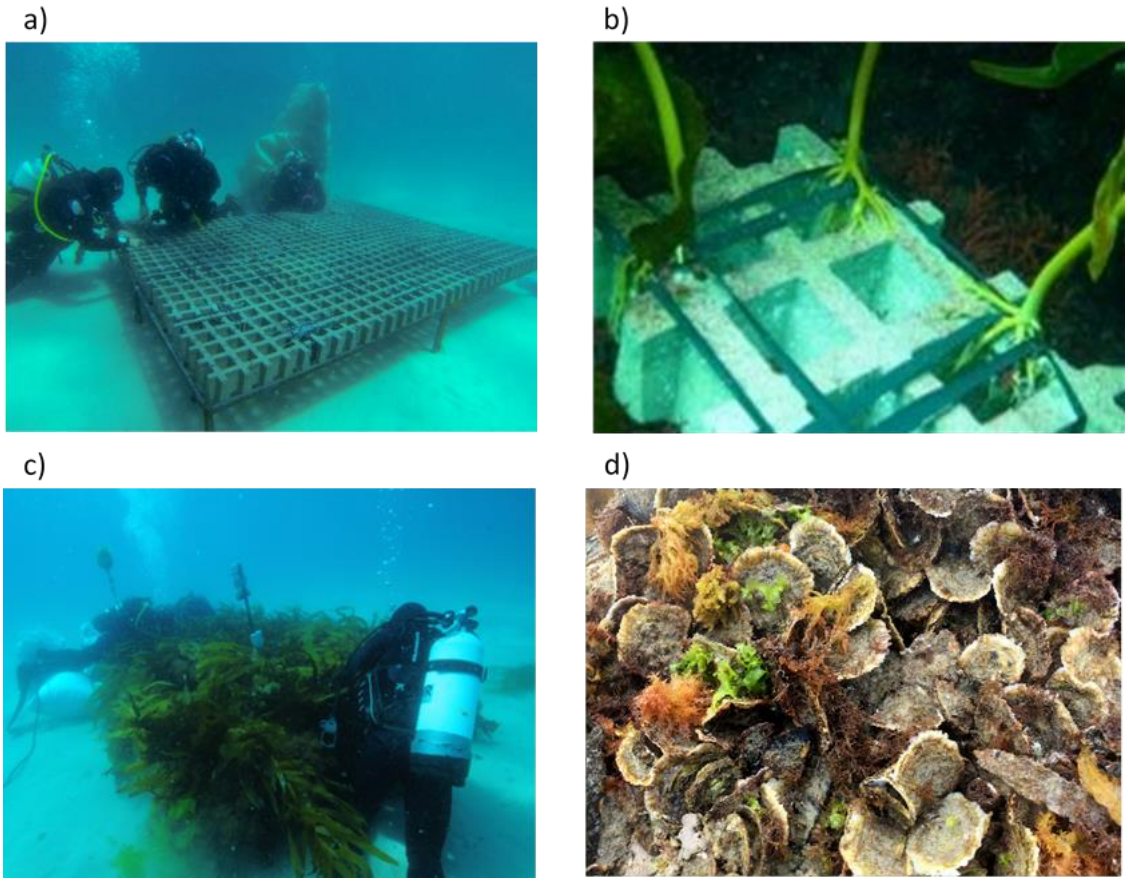

Figure 3.1. Images highlighting a) construction of the experimental reefs at ~ 6 m depth by divers, b) kelp transplanted to the concrete pavers, c) an experimental reef with a high density of kelp after ~ 12 months, and d) the high density of oysters that naturally recruited to reefs supporting kelp.

3.4.2 Benthic oyster density

The density of *Ostrea angasi* that naturally recruited to reefs was determined using photo quadrats of the reef surface taken 5 and 24 months after the reefs were deployed (in May 2015 and in December 2016), providing an assessment of the initial establishment of recruits (following the summer recruitment period) and their subsequent persistence on the reefs (Fig. 3.1d). In May 2015, this involved capturing 0.12 m^2 of reef surface in 1 - 4 different

randomly selected locations (one photo for 0.12 & 0.24 m^2 reefs, two photos for 0.48 m^2 reefs and four photos for the larger reef sizes), pushing aside any algae obscuring a view of the benthos. Prior to taking photographs in December 2016 at the end of the experiment (at 24 months), we removed the understory algae from either the entire reef surface (for reefs < 1 m^2) or from a 1 m^2 area positioned in the north-east corner of each reef (for reefs > 1 m^2). We then photographed the area from which the algae were removed using multiple images each 0.12 m^2 in area. The density of oysters at both times was determined by counting the number of oysters within the image (results where averaged across photo quadrats from the same reef).

3.4.3 Benthic biomass estimates

When dismantling the reefs at the end of the experiment, we collected an individual paver from the centre of each of the largest reefs (7.68 m^2) i.e. across the four kelp densities. Oysters colonising both the upper and lower surface of these pavers were removed with hand tools and placed into separate (labelled) zip-lock bags for later analysis. The shell length of each 'live' oyster was measured using electronic hand callipers and these measurements were used to estimate the biomass of oysters (using the formula: $\text{weight}=0.0002 \times \text{length}^{2.8924}$ (Jones 2016), which was developed for *O. angasi* in similar environmental conditions to our study site).

3.4.4 Above canopy oyster recruitment

The abundance of oysters recruiting immediately at the canopy height of *E. radiata* was determined by counting the number of *O. angasi* recruits present in larval collectors tethered to the centre of each reef (Fig. 3.4b). Each water column collector consisted of a cylinder of black oyster mesh (length = 1 m, diameter = 0.35 m), which was filled with plastic bio-balls

used as pond filtration media (unbranded, 40 mm diameter) that served to provide complex habitat structure (Ammann 2004). The collectors were retrieved in March 2016 (at 15 months, when there was a peak in recruitment), after a six-week deployment period. Divers placed the collectors in 500 µm mesh bags and the samples were processed back on land. Processing involved separating all the invertebrates from the bio-balls and oyster mesh, which was achieved by thoroughly rinsing the mesh under a hose and immersing and agitating the bio-balls in a bucket of fresh water. The water was then passed through a 500 µm sieve to separate out the invertebrates. Invertebrates were preserved in 70% ethanol (to water) and the number of complete *O. angasi* shells was enumerated back in the laboratory.

3.4.5 Biotic and abiotic factors

The potential influence of abiotic factors, competition from sessile species, and predation by mobile species on *O. angasi* recruitment were explored. Relationships between the density of *O. angasi* recruits and abiotic variables were determined using abiotic measurements presented in Layton et al. (2019b): sub-canopy irradiance, measured as a percentage of above canopy irradiance using a LI-COR light sensor; sub-canopy water flow, measured as a percentage of above canopy flow determined by clod card dissolution rates; sub-canopy sediment deposition, measured as a percentage of above canopy rate of deposition determined by sediment traps; and sediment accumulation, measured as the depth of accumulated sediments of the reef surface. Light was measured in November 2015, flow and sediment deposition measurements were averaged across multiple seasons in 2015 and sediment accumulation measurements were averaged across September 2015 and January 2016. Relationships were also derived between the density of *O. angasi* recruits and the percentage cover of sessile species: all understory algae, foliose algae (Appendix A: Fig. A. 1a), and turf forming algae (Appendix A: Fig A. 1c) measured from photo-quadrats taken in May 2015

and December 2016 (the same quadrats used to assess oyster density). And finally, relationships between the density of *O. angasi* recruits and the density of 'large' mobile macroinvertebrates (> approximately 50 mm) and fishes associated with the reefs were assessed. Macroinvertebrates and fishes were assessed through visual surveys conducted *in situ* with the same diver recording the abundance of species on and immediately surrounding each reef across all four seasons (between November 2015 and December 2016). The total abundance of fishes and invertebrates was then converted to density by dividing abundance by reef area, and results for each season were averaged to yield an annual average density.

3.4.6 Analyses and Statistics

The effect of kelp density (fixed factor) and patch size (covariate) on the density of *O. angasi* on the reefs in May 2015 (at five months) and at the end of the experiment in December 2016 (at 24 months), as well as the abundance of recruits in the collectors above the canopy in March 2016 (at 15 months), were determined using Analysis of Covariance (ANCOVA) based on routines in R (version 3.2.4). Model assumptions were checked using diagnostic plots (for normality, linearity and homoscedascity), model residuals (for linearity and homoscedascity), and the Shapiro-Wilks normality test. Data transformations were based on the λ coefficient at the maximum log-likelihood plot produced using the Box-Cox procedure. The covariate (patch size) was $\log_2$ transformed as this improved model assumptions and patch size increased on (approximately) a $\log_2$ scale. Homogeneity of slopes was tested by fitting the saturated model including the interaction term, before the unsaturated model without the interaction term was fitted when this assumption was upheld. When appropriate saturated models not showing homogeneity of slopes were re-analysed after dropping the least homogenous treatment. Figures using untransformed data were produced using the *ggplot2* package. Where a significant effect of kelp density was detected, pairwise

comparisons of covariate adjusted means with a Bonferroni adjustment of significance (to correct for multiple testing) were performed (Quinn and Keough 2002) using the *lsmeans* and *multcomp* packages.

Regression and multiple regressions were used to assess the influence of abiotic (light, flow, sediment deposition and sediment accumulation) and sessile species (the cover of turfing algae, foliose algae and all algae combined), as well as mobile species (the annual average density of macroinvertebrates and fishes) on the density of *O. angasi* in May 2015 and December 2016. Separate analyses were performed for each of the two response variables where the effects of the four abiotic and the two biotic predictor variables (percent cover of sessile species, density of mobile species) were first analysed separately and then in combination. To avoid the effect of inflated oyster density values for reefs < $1m^2$ (where densities would need to be standardised by scaling up), these analyses only included data from the four largest reefs (1.08 - 7.68 m^2). Normality, linearilty and homogeneity of variance were investigated with a scatterplot matrix and diagnostic plots (as outlined for ANCOVA). Multi-colinearity was investigated through pairwise correlations and the variance inflation factor of the variables. In order to address multi-colinearity, the effects of highly correlated terms were separately assessed, and then the term which had the lowest explanatory power was excluded from further analysis. Model selection was achieved by comparing the fit of all possible models for each response variable (Quinn & Keough 2002) using AIC (Akaike's information criterion) and the *leaps* package. Hierarchical partitioning was then used to determine the independent contribution of each of the predictor variables considered in each multiple-regression model using the *hier.part* function. We then determined the likelihood that the independent contribution could be due to chance by

performing a randomization test and assessing the significance of the *Z* scores at the 95% confidence level.

3.5 Results

3.5.1 Benthic recruitment

The density of *Ostrea angasi* in May 2015 was affected by a significant patch size x kelp density interaction (ANCOVA; $F_{(3,20)} = 3.42$, $P = 0.037$; Fig. 3.2a, Appendix A: Table A. 1). There was negligible recruitment across reefs without kelp, whilst 100 - 500 oysters/m^2 were present on the larger reefs (≥ 1.08 m^2) with kelp. Omitting the reefs with zero kelp removed the interaction and revealed significant independent effects of patch size and kelp density, where oyster density increased with patch size (but appeared to level off for reefs ≥ 1.08 m^2), and reefs with low densities of kelp had significantly more oysters than reefs with high kelp densities (Appendix A: Table A. 1).

The densities of *O. angasi* were also observed to increase significantly with patch size and kelp presence in December 2016 (Fig. 3.2c, Appendix A: Table A. 1). Although, much greater densities of oysters were recorded on the reefs without kelp at this time than previously (up to approximately 100 individuals/m^2), however these reefs still had significantly lower oyster densities than the reefs with kelp.

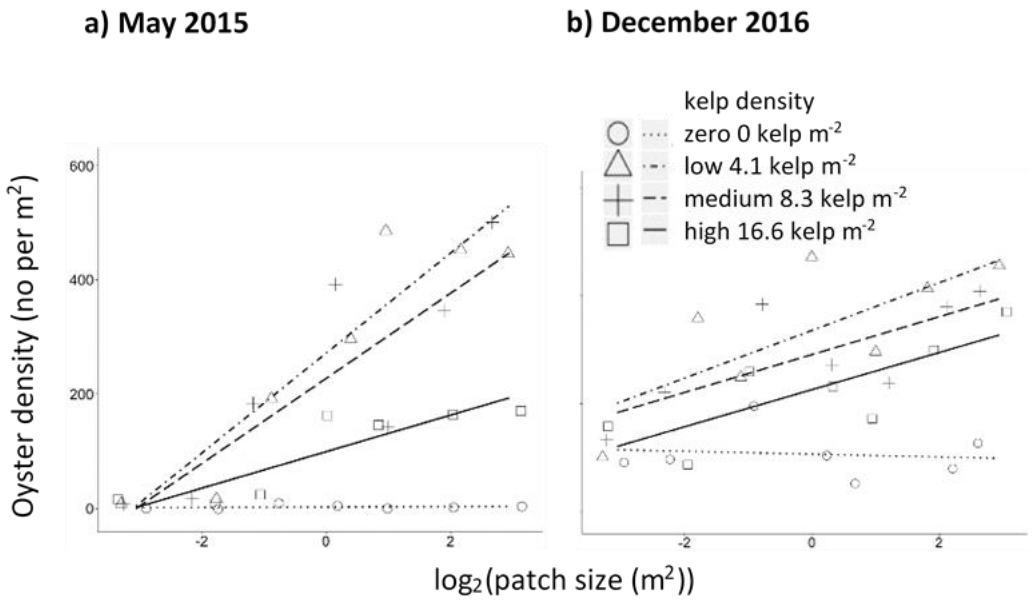

Figure 3.2. Density of *O. angasi* on reefs of different patch size and kelp density in a) May 2015 and b) December 2016 (5 and 24 months after reef installation).

3.5.2 Benthic oyster biomass

The size distributions of oysters on the top and bottom of pavers and among kelp densities (where patch size = 7.68 m^2) (Fig. 3.3a) were reasonably consistent across kelp density and generally ranged between 30 and 70 mm; however, estimated biomass was approximately four times greater on the top surface of the pavers compared to the underside due to much higher densities (Fig. 3.3b).

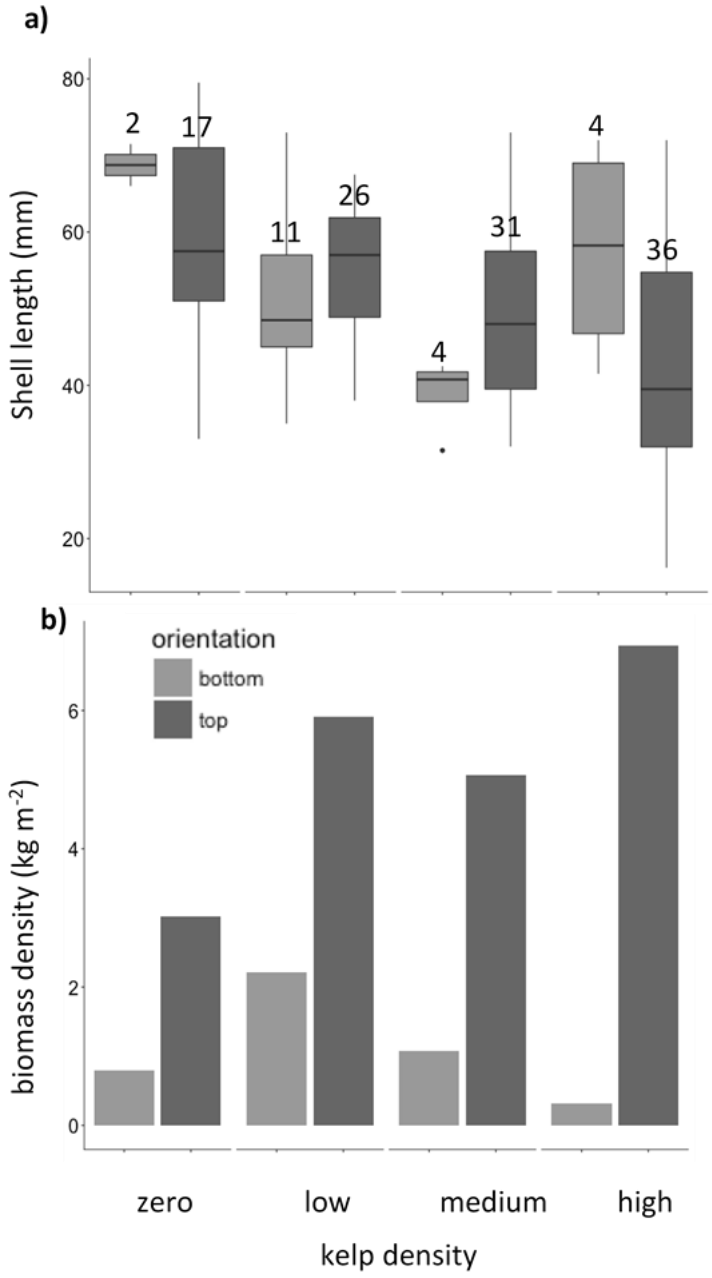

Figure 3.3a) Box and whisker plots for oyster shell length, and b) estimates of oyster biomass on the top and under surface of reef substratum (concrete pavers) on the largest reefs (7.68 m^2) at each kelp density. Numbers above whiskers refer to the number of oysters that were measured. Biomass estimates were based on shell length measurements and calculated by the relationship: weight = 0.0002 x $length^{2.8924}$ (Jones 2016).

3.5.3 Above canopy oyster recruitment

The number of *O. angasi* recruits present in water column collectors appeared to decline slightly with patch size and reefs with low densities of kelp appeared to have increased recruitment compared to other densities (Fig. 3.4a). Reefs without kelp had a similar number of recruits to many of the reefs that supported kelp, which contrasted with oyster density at the benthos. However, patch size was marginally non-significant (ANCOVA; $F_{(1,23)} = 4.14$, $P = 0.054$), whilst kelp density was significant (ANCOVA; $F_{(3,23)} = 3.05$, $P = 0.049$), but the post-hoc tests didn't reveal any significant pairwise comparisons (Appendix A: Table A. 1).

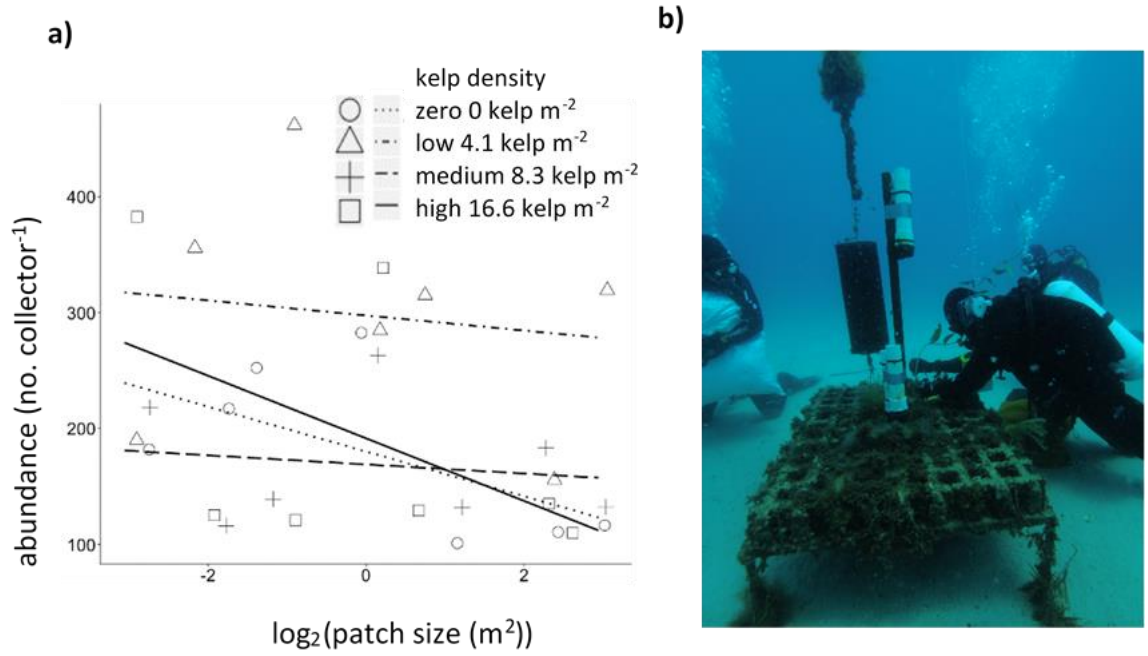

Figure 3.4a) The number of *O. angasi* within larval collectors on reefs of different size and supporting different kelp densities. b) An image highlighting the larval collector positioned at kelp canopy height on a reef without kelp transplants.

3.5.4 Abiotic and biotic factors

On their own, mobile species (macroinvertebrates and fishes) were poorly and non-significantly correlated with oyster density at both times (5 and 24 months, Appendix A: Table A. 2). The best abiotic model explaining the influence of *E. radiata* on the density of *O. angasi* recruits in May 2015 (at five months) combined light and sediment deposition and

had similar predictive power to the simpler biotic model, where total algal cover was the only predictor variable identified (adj. r^2 = 0.68 & 0.66 respectively; Appendix A: Table A. 2). The optimal modal combining both abiotic and biotic factors included light, sediment deposition total algal biomass, and macroinvertebrate density (non-significant) which explained 81% of the variability in the data, but the hierarchical partitioning showed that sediment deposition (6%) and macroinvertebrates (5%) had much lower independent contributions than light (38%) and algal biomass (38%).

The best abiotic model explaining the density of *O. angasi* recruits in December 2016 (at 24 months) included light and sediment accumulation (74%) but had less predictive power than the biotic model which only used turf percentage cover (81%) (Appendix A: Table A. 2). As light and turf cover were highly correlated, they couldn't be combined into a single model. The optimal model combining both biotic and abiotic factors included turf cover and macroinvertebrate density (85%), with both factors having significant independent contributions (turf = 51% macroinvertebrate = 25%).

3.6 Discussion

Ostrea angasi dominated the benthos on all reefs supporting transplanted *Ecklonia radiata* but were much less abundant on reefs without the kelp, suggesting a strong facilitative effect of *E. radiata*. Furthermore, *E. radiata* structure influenced the degree of the facilitation, with larger patch sizes supporting low or medium kelp densities providing the most favourable conditions for oysters. As the abundance of recruits in water column collectors didn't differ significantly between reefs with and without kelp, variability in recruit abundance at the benthos likely resulted from differing sub-canopy conditions, rather than spatial variability in

larval concentration (including variability caused by auditory and chemical settlement cues which operate at scales beyond the canopy height of *E. radiata*). However, there may still be some contributory (but obscured) effects of conspecifics on *O. angasi* recruitment (e.g. through positive chemotaxis) (Bayne 1969). The mechanism by which *E. radiata* influences *O. angasi* recruitment is likely to be complex, but the most important factors appeared to be their capacity to reduce benthic light and turfing algal cover. However, there may have also been an additional influence of mobile macroinvertebrates on post-settlement survival, as well as other factors that require further investigation. The dense coverage of oysters that occurred on many reefs within just two years highlights the potential for these findings to assist the restoration of *O. angasi*-based systems.

To our knowledge subtidal macroalgae have not been shown previously to facilitate oysters. Nor could we find any evidence relating to the co-occurrence of *E. radiata* and *O. angasi* in the literature. We did however observe sparse numbers of *O. angasi* occurring naturally both within *E. radiata* forests at Maria island and on surrounding areas of sand. The only sizable reference ecosystem for *O. angasi* occurring in Australia (Georges Bay Tasmania) is practically devoid of kelp, demonstrating that kelp are clearly not a prerequisite for *O. angasi*, although on our artificial reefs they enhanced their establishment. Other kelp species have been shown to have a detrimental effect on oysters (Kochmann and Crowe 2014) and macroalgae are generally negatively associated with bivalves (Witman 1987). Kelp may outcompete oysters for space, provide a physical barrier to their larvae, increase sediment stress, and abrade/dislodge recruits (Albrecht and Reise 1994, George 1999, Jenkins and Hawkins 2003). However, co-habitation and possible mutual facilitation between macroalgae (or salt marsh) and bivalves occurs intertidally where both species have complementary effects on local biodiversity (Altieri et al. 2010, Hughes et al. 2014, Vozzo and Bishop 2019).

The use of kelp to help restore oyster reefs has not been attempted, but given the valuable ecosystem services provided by both species, including their capacity to enhance surrounding marine habitats (e.g. oyster improving water quality for nearby seagrass meadows (Wall et al. 2008) and kelp providing detrital subsides on and off-shore (Steneck et al. 2002)), there are likely to be added benefits of combining the restoration of kelp and oysters, although tradeoffs in their ecosystem services may occur when restored together. However, as the cost of kelp forest restoration far exceeds that of oyster reefs (McLeod et al. 2018), there may be more cost-effective alternative to harness the beneficial effects of kelp to restore oyster reefs.

3.6.1 Facilitation by kelp

Although the physical structure and the deployment (timing, location) of the reefs, likely influenced their suitability for colonisation by oysters (see *Implications for practice*); the kelp was critical in determining the level of recruitment. *E. radiata* appeared to facilitate *O. angasi* through their capacity to modify both abiotic and biotic factors, with sub-canopy light and understory algae (including turf cover) appearing to have dominant negative influences on recruitment at 5 and 24 months. High light at the benthos may lead to lower settlement of larvae compared to low light (either by low light positively affecting settlement or high light negatively affecting settlement) and light may also be indirectly associated with mortality of newly settled recruits (Young and Chia 1984). Little is known about the recruitment preferences of *O. angasi*, however, the closely related species *Ostrea edulis* is negatively phototactic (Bayne 1969), which is a characteristic it likely shares with *O. angasi*.

At 5 months, *O. angasi* was negative associated with understory algal cover of any type, whilst at 24 months, turf cover was the strong negative correlate. *O. angasi* settlement may therefore depend on the availability of hard substrata (Smyth et al. 2017), which can be

reduced rapidly by pioneering benthic algae (of all types). But, as algal communities develop over time, it is primarily the turf-forming species that continue to have a detrimental impact on post-settlement survival and subsequent recruitment. Miller and Etter (2008) found that the negative relationship between invertebrate recruitment and light can result from increased post-settlement mortality caused by competition for space with algae, which are more prevalent under high light, and not any direct effect of light *per se*. However, given the strong influence of light on the settlement of *O. edulis* (Bayne 1969), combined with the fact that light had a strong contribution to variability in the density of *O. angasi*, both factors are likely to effect the establishment of *O. angasi* populations.

Apart from through competition for space, turfs may inhibit oyster recruitment through their capacity to trap sediment (Connell et al. 2014), which provides an unstable surface for larval attachment and may smother vulnerable new settlers. Algal turfs may also form a chemically distinct boundary layer that could subject colonising invertebrates to strong pH and oxygen fluctuations (Larkum et al. 2003, Layton et al. 2019a). Furthermore, due to their low height, turfs may also increase exposure to the unameliorated abiotic stressors, (e.g. high water flow and shear stress (Eckman and Duggins 1991) compared to other algal growth forms which may provide a buffering effect. These factors are likely to assist turfs in maintaining a competitive dominance over oysters and other benthic species where conditions are suitable for their establishment. The ability of kelp to suppress the development of turfs through canopy shading, as well as by removing sediments and damaging small understory algae by benthic sweeping, is therefore likely to have been a crucial part of *Ecklonia's* faciliatory effect on *O. angasi*.

Light and competition with understory algae do not explain the reduced density of *O. angasi* on reefs with a high density of kelp compared to those with intermediate densities. This could result from increased post-settlement mortality of oysters caused by elevated macroinvertebrate densities on reefs with high densities of kelp (compared to those with intermediate densities) (Appendix A: Table A. 2), however, we did not investigate which species were consuming *O. angasi* recruits (if any), nor did we conduct predator exclusion experiments which would help determine their impact. It is also possible that some recruitment drivers had non-linear effects on *O. angasi* establishment. For example, it is possible that only the highest level of sediment deposition, which occurred on reefs with the highest kelp density, detrimentally impacted *O. angasi* recruitment. Alternatively, intermediate kelp densities could have promoted high settlement of oyster larvae through an optimised reduction in water flow, whilst high densities of kelp could have provided a partial barrier to the transfer of larvae to the interior of the reef resulting in reduced recruitment. Further manipulative experiments are required to determine the separate and combined effects of various abiotic and biotic factors on *O. angasi* settlement and post-settlement survival and to better resolve why different kelp densities had different effects on *O. angasi* recruitment.

Although foliose algae cover at 24 months was positively correlated *with O. angasi* density (excluded from further analyses due to collinearity with turfs, but see Appendix A: Fig. A. 1) and showed a similar response to kelp density, we do not believe that foliose algae were a driver of oyster recruitment. Instead, turfs probably had a negative impact on both foliose algae and oysters, as most of the foliose algae established after the initial recruitment of *O. angasi* and foliose algae were observed growing directly on the reef surface as well as on oysters, but not in areas dominated by turfs. It is unclear whether *O. angasi* enhanced the

establishment of foliose algae in any way, nor can we determine whether the prior establishment of large foliose algal species will have the same detrimental effect on oyster recruitment as more prostrate pioneering species.

3.6.2 Implications for practice

Over-dominance of turfing algae inhibiting the recruitment of other species is a ubiquitous problem in the marine environment (Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018) and could be linked to the demise of *O. angasi* in parts of Australia. Turf proliferation is likely to occur following the loss of kelp habitat (Filbee-Dexter and Wernberg 2018) and may be promoted through the creation/deployment of new hard substratum, which often occurs with shellfish reef restoration. Therefore, combining conventional approaches to restore oyster reefs with strategies that suppress turfs (e.g. mixed species restoration including species that inhibit turfs such as kelp or potentially mobile grazers such as sea urchins), could benefit restoration in many locations. A more cost-effective means than using kelp to reduce benthic light and suppress turf growth could be to shade the benthos using artificial means (e.g. with shade cloth or a kelp surrogate) until oysters are able to successfully establish and become resistant to turfs. Alternatively, it could be worthwhile piloting *O. angasi* restoration projects within existing kelp forest. More research is needed to identify techniques which facilitate high recruitment of oysters and can effectively translate to restoration practice.

The physical characteristics of the concrete pavers used in this experiment are likely to have also influenced *O. angasi* recruitment. The holes in the pavers could have provided a refuge for recruits from high sedimentation, light, competition from algae, and predators. Indeed, on reefs without kelp, oyster recruitment was largely confined to the holes. Artificial substratum

presently used in restoration such as concrete rubble and shell clutch is likely to provide similar refugia for recruits. Oysters were also less numerous on the underside of the pavers compared to the tops. This may be due larval settlement behaviour or relate differences in post-settlement mortality. Regardless of the mechanism, the provision of downwards facing surfaces is unlikely to provide additional benefit to restoration.

Although not explicitly tested, other aspects of the reef infrastructure, the timing of their deployment, and the site location, may have enhanced recruitment of *O. angasi* and therefore warrant consideration. The site location we used may be a strong candidate for *O. angasi* reef restoration projects due to the high levels of natural recruitment, which was probably influenced by the relatively pristine water quality and the surrounding patchy populations of *O. angasi* (at Maria island). We believe that there are likely to be numerous locations across Australia, where conditions are suitable for *O. angasi* to establish, but most will lack a sufficient natural supply of recruits. Secondly, the fact that the reefs were installed at the time of year when *O. angasi* were recruiting may have allowed oysters to establish before many of their competitors. It may therefore be prudent to deploy artificial substratum just prior to the recruitment period to minimise detrimental effect of competitors. And finally, the modular structure of the reefs used in this experiment is likely to be suitable for transport and deployment in other locations. This presents a potential opportunity to utilise beneficial locations and the facilitative effect of kelp to establish oysters on reefs, and then use these reefs to catalyse *O. angasi* restoration in other areas. Facilitation should receive careful consideration in marine restoration. We identified a potential beneficial association between oyster reefs and kelp which warrants further investigation.

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Chapter 4. Kelp patch size and density influence secondary productivity and diversity of epifauna

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4.1 Abstract

Habitat-forming ecosystem engineers are the foundation of many marine ecosystems where they support diverse and productive food-webs. A reduction in their patch size or density may affect the productivity, biodiversity, and stability of these ecosystems. We determined the effects of different densities and patch sizes of *Ecklonia radiata* (the dominant kelp in southern Australia) on the secondary productivity, species richness, diversity, and community structure of understory epifaunal invertebrates and how associated environmental covariates modified by kelp affected those patterns. We assessed sub-canopy epifauna across 28 artificial reefs with transplanted *E. radiata* consisting of seven different patch sizes (0.12 – 7.68 m^2) crossed with four kelp densities (0 – 16 kelp m^{-2}) over two years. Epifaunal secondary productivity associated with both natural algal and standardised rope fibre habitats decreased with patch size and was elevated when kelp was absent, however, it was also high in natural habitat when there was a high density of kelp. Epifaunal productivity was positively associated with sub-canopy light and water flow but negatively associated with the biomass of the dominant understory alga, *Ulva*. sp. Epifaunal diversity declined with decreasing reef size as did richness which correlated with a loss of algal species richness. Community structure of epifauna also differed between small and large reefs, between reefs with and without kelp, between rope habitats at the centre and at the edge of reefs, and within natural habitat between reefs supporting high and low densities of kelp. Overall, these results indicate complex effects of *E. radiata* decline on epifaunal communities, with high secondary productivity associated with dense kelp stands, but also areas without kelp that are dominated by turf algae. While the loss of standing kelp from rocky reefs may result in declines in epifaunal biodiversity, where turf algae replaces kelp, the reefs may still support high secondary productivity.

KEY WORDS: secondary productivity; ecosystem engineer; understory algae; turf algae; *Ulva; Ecklonia radiata*

4.2 Introduction

Degradation in the patch size and structure of habitat-forming ecosystem engineers is likely to strongly affect trophic dynamics, biodiversity and ecosystem function. Canopy-forming seaweeds of the orders Laminariales and Fucales, hereafter collectively referred to as 'kelp' (see Steneck and Johnson (2014)) are foundation species on temperate rocky reefs and support extremely productive and diverse coastal food webs (Smale et al. 2013, Coleman and Wernberg 2017). They provide complex habitat structure and exert strong influences on the abiotic (e. g. light, sedimentation, water flow) and biotic (e.g. other algae and sessile invertebrates) environment (Teagle et al. 2017, Layton et al. 2019b). As primary producers, kelp contribute to trophic interactions directly through living and decaying tissue being consumed by herbivores and detritivores. Kelp also shape coastal food webs indirectly by modifying abiotic factors which influences the production of other algal species (Miller et al. 2011), the localised delivery and retention of phytoplankton and detrital resource subsidies (Miller et al. 2015), as well as the abundance, species composition, and behaviour of consumers across multiple trophic levels (Graham 2004). Ecosystem engineers such as kelp have a critical role in shaping trophic dynamics, however, there is a need to better understand and account for the indirect effects of ecosystem engineers on food webs (Sanders et al. 2014).

Kelp density and patch size varies naturally at both local and regional scales (Dayton 1985b), but both are being increasingly modified by escalating environmental stressors including

increasing temperature, sedimentation, competition from algal turfs stimulated by additional nutrient loading, epibiosis, and overgrazing (Steneck et al. 2002, Ling et al. 2009a, Wernberg et al. 2013, Sogn Andersen et al. 2019). Kelp loss affects the abiotic environment beneath the canopy, resulting in an increase in benthic light, water flow, and sediment accumulation, and decreases in oxygen concentration, particle deposition, and benthic scour by kelp laminae (Kennelly 1989, Layton et al. 2019b). These abiotic factors then influence the recruitment and development of understory algal and sessile invertebrate assemblages (Wernberg et al. 2005, Flukes et al. 2014), which may further shape kelp forest community dynamics. There are some consistent effects of kelp canopy structure on understory algae, in particular the absence of a canopy is often associated with a high dominance of filamentous algal turfs (Filbee-Dexter and Wernberg 2018), and in Australia there is some evidence that canopy thinning can increase the dominance of sub-canopy foliose algae (Flukes et al. 2014). However, understory algal assemblages are often highly complex and variable. Because understory algal habitats support diverse communities of mobile epifauna (e.g. gastropods, amphipods, bivalves, decapods) (Seed and O'Connor 1981), changes to the abiotic sub-canopy environment, along with changes to the structure of understory algal communities are likely to influence the overall productivity and diversity of kelp ecosystems.

The abundance and diversity of epifaunal invertebrates are pivotal to secondary production and the availability of resources for higher trophic orders (Taylor 1998), especially fishes (Edgar and Shaw 1995a), in coastal food webs. Secondary productivity of epifaunal communities tends to be limited by a quantifiable resource ceiling (Edgar and Aoki 1993), which is determined by the production of both micro-and-macro-algae, but supplemented by additional planktonic and detrital food resources (Duggins et al. 1989, Miller et al. 2011). However, given that kelp canopy structure influences multiple factors that determine the

availability of resources for sub-canopy epifauna, it is difficult to predict overall effects of changes in kelp cover on epifaunal productivity and community structure.

Kelp forest epifauna have a variety of feeding strategies, which may affect how the abiotic environment of the sub-canopy influences secondary productivity and community development. For example, epifaunal species that feed predominantly on plankton and detritus, are likely to respond strongly to drivers such as hydrodynamics and particle deposition, resuspension and accumulation rates (Edgar 1983a). By contrast, species that feed predominantly on algae and microphytobenthos (hereafter MPB) may respond more strongly to light availability due to its effect on algal production (Edgar 1983a). Furthermore, epifaunal abundance is also strongly influenced by their algal habitat, which not only affects food resource availability, but also provides a refuge from predators (Duffy and Hay 1991, Wright et al. 2014). In particular, algae with convoluted surfaces, complex branching structures, and extensive epiphyte cover tend to support more abundant and diverse communities of epifauna (Seed and O'Connor 1981, Hacker and Steneck 1990, Eilertsen et al. 2011). Algal species richness and diversity also tend to be weakly associated with epifaunal richness and diversity (Parker et al. 2001).

To better understand the consequences of increasing modification to kelp habitat on an important component of rocky reefs communities in temperate Australia, we experimentally assessed the effect of different densities and patch sizes of the dominant canopy-forming kelp, *Ecklonia radiata,* on secondary productivity, species richness, diversity, and community structure of understory epifaunal invertebrates. This was done by establishing *E. radiata* on artificial reefs at different densities and patch sizes for two years and estimating secondary productivity of epifauna associated with both natural algae and a standardised artificial

habitat within the kelp on these reefs. We also investigated how differences in ecosystem engineering by *E. radiata* influenced epifaunal productivity by determining the relationships between epifaunal productivity, and abiotic factors (sub-canopy light levels, water flow, sediment deposition, and sediment accumulation) and biotic factors (the biomass of different algal functional groups and the percentage cover of sessile invertebrates) modified by *E. radiata*. Finally, we identified how epifaunal responses to changes to density and patch size varied with feeding strategy.

4.3 Methods

4.3.1 Study system

Ecklonia radiata is the dominant canopy-forming kelp across southern Australia and is the foundation species of biodiverse and productive food webs. It typically grows to < 1.5 m tall and can form forests down to a depth of 60 m. Similar to many kelp forests globally, *E. radiata* is subject to escalating environmental stressors, which is causing this species to become sparser and more patchily distributed in some locations (Connell et al. 2008, Ling et al. 2009a, Johnson et al. 2011, Wernberg et al. 2016).

Experiments were conducted off the west coast of Maria Island in south eastern Tasmania, Australia, utilising an array of 28 artificial reefs varying in size and supporting *E. radiata* transplanted at different densities, as described in Layton et al. (2019b). An analysis of covariance design was applied, with all combinations of seven different patch sizes (0.12, 0.24, 0.48, 1.08, 1.92, 4.32, 7.68 m^2) crossed with four kelp densities (0, 4.1, 8.2 and 16.4 kelp m^{-2}). Reefs were deployed across a flat sandy substratum of uniform depth (6.5 m) in an approximately square grid, over 1.5 km from the nearest natural reef and with a distance of

25 m separating the reefs. Densities represented the average density of *E. radiata* in nearby reefs (8.2 kelp m^{-2}), half that density (4.1 kelp m^{-2}), twice that density (16.4 kelp m^{-2}) and no kelp at all (0 kelp m^{-2}). All these densities (hereafter referred to as: zero, low, medium, and high kelp densities), exist in naturally heterogeneous *E. radiata* forests in southern Australia. The reef infrastructure was deployed in December 2014 and adult kelp were first transplanted to the reefs in January/February 2015 by securing holdfasts to the reef surface with large rubber bands which facilitated attachment of the holdfast to the reefs (Layton et al. 2019b). Treatments were maintained on the reefs for two years (until December 2016). During this time kelp densities were maintained by replacing losses at regular intervals (approximately every six weeks) with fresh transplants from a nearby collection site. Once the kelp treatments were established, communities of other algae, fish, and invertebrates soon proceeded to establish naturally on the reefs.

4.3.2 Secondary productivity

Two methods were used to assess secondary productivity and composition of epifauna associated with the understory of the reefs (described in detail below). The first method examined epifauna that established themselves on standardised rope fibre habitats (hereafter RFH) (Edgar 1991a, Edgar 1991b), which were used to investigate the influence of kelp density and patch size independent of the influence of understory algal habitat structure. The second method examined epifauna that established in the natural understory algal habitat (hereafter natural habitat (NH)), which was achieved by destructively sampling the understory algae and associated mobile invertebrates from each reef at the conclusion of the experiment using a suction device.

4.3.3 Rope fibre habitats (RFH)

RFH were deployed from April until November 2015 in two positions on each reef; in the centre and on the northern edge directly exposed to incident light. The two locations allowed for examination of edge effects in addition to patch size and density effects. Following the experimental soak period, RFHs were collected in individual bags and transported to the lab in a coolbox with seawater. Secondary productivity of epifauna on each RFH was estimated using the sieve-size-fractionation method (Edgar 1990c) with the following sieve aperture sizes: 1.0, 1.4, 2.0, 2.8, 4.0 mm. Invertebrates were separated from the rope fibre by the addition of ethanol (approximately 30 ml) to the bags, and teasing the fibres apart after thorough mixing. The RFH and dislodged invertebrates were then washed over the stacked series of sieves. Animals retained on each sieve were transferred to a petri dish and the abundance of different taxonomic groups enumerated. Most taxa were classified to species or genus (for amphipods) with a few taxa only classified to class (Appendix B: Table B. 1). The abundance of different taxa retained on the different sized sieves allowed for estimates of biomass (based on established relationships between the size of different taxa and their AFDW (ash-free dry weight) Edgar (1990c)). Secondary productivity was then derived from biomass estimates using taxon-specific variants of the equation: Productivity = 0.0049 * $Biomass^{0.80}$ * $Temperature^{0.89}$ (which relates biomass to growth rate), and using the water temperature at time of collection (14 °C) (Edgar 1990c). Secondary productivity estimates were summed across all individuals to estimate community level productivity. Taxa were also assigned to feeding strategies (Appendix B: Table B. 1) and the productivity for each 'feeding group' determined.

4.3.4 Natural habitat (NH)

Secondary productivity of epifauna associated with NH was assessed in December 2016. This involved carefully removing understory algae from the reef surface using scrapers, a wire

brush and an air-driven venturi suction sampler fitted with a 500 µm mesh collection bag. The algae and associated epifauna were collected from the entire reef surface for reefs < 1 m^2, or from a 1 m^2 quadrat positioned in the north-east corner of the reef for reefs >1 m^2. Samples were frozen and stored for later analysis. Processing involved gently thawing the samples and separating the invertebrates from the algae in freshwater trays. The algal samples were processed separately and sorted into distinct taxa. Secondary productivity was assessed for invertebrates separated from algae as described above for RFH.

4.3.5 Abiotic and biotic factors

Relationships between secondary productivity and four abiotic variables engineered by *E. radiata* (sub-canopy light, water flow, sediment deposition and sediment accumulation) were determined using data described in Layton et al. (2019b). These variables were measured at multiple times on these reefs over the two years of the experiment, where sub-canopy light was measured as the percentage of above canopy light using a LI-COR LI-1500 Light Sensor Logger and a Spherical Underwater Sensor; sub-canopy flow was measured as a percentage of above canopy flow using clod card dissolution rates; sub-canopy sediment deposition was measured as a percentage of above canopy rate of deposition using sediment traps; and sediment accumulation was the measured depth of the turf-sediment matrix on the reef surface. Briefly, these data showed declines in irradiance, water flow, and sediment deposition, but an increase in sediment accumulation with increasing *E. radiata* patch size and density (Layton et al. 2019b). We used below canopy measurements relative to the above canopy measurements as we were interested in assessing how differential engineering effects associated with different densities and patch size related to epifaunal secondary productivity.

Relationships between secondary productivity of epifauna and algal host characteristics were determined using biomass (dry weight) of six algal groups: filamentous algae, branching corticated algae, foliose algae, leathery macrophytes, the most abundant non-kelp species (i.e. *Ulva* sp.), and all understory algae (all determined from destructive sampling in December 2016).

4.3.6 Analyses

The effects of kelp density (fixed factor) and patch size (covariate) on epifaunal secondary productivity, species richness, and diversity, within NH were analysed by Analysis of Covariance (ANCOVA) using R (version 3.2.4). ANCOVAs were also run for RFHs but included an additional fixed factor, habitat position (edge or centre). Model assumptions were checked by diagnostic plots (for normality, linearity, and homoscedascity), model residuals (for linearity and homoscedascity) and the Shapiro-Wilks normality test. Data transformations were based on the maximum λ coefficient from log-likelihood plots produced using the Box-Cox procedure. The covariate patch size was $\log_2$ transformed to linearise the data (patch size increased on an approximate $\log_2$ scale). Homogeneity of slopes was assessed by fitting the full model including the interaction term, and when the interaction term was insignificant the model without the interaction term was fitted. Figures using untransformed data were produced using the *ggplot2* package. When significant effects of kelp density occurred, pairwise comparisons of co-variate adjusted means were performed with a Bonferroni adjustment of significance (to correct for multiple testing) (Quinn and Keough 2002) using the *lsmeans* and *multcomp* packages.

The community structure of epifaunal invertebrates was analysed using PRIMER 6. Multi-dimensional scaling (MDS) plots highlighted variation in the community structure with patch

size, kelp density and (when relevant) habitat position. Canonical analyses of principal coordinates (CAP) plots were also undertaken to highlight differences in epifaunal communities with kelp density accounting for variability caused by patch size. From an initial MDS plots of all data relating to each sampling method (Appendix B: Fig. B.1), we divided reefs into *small* (≤ 1.08 m^2) and *large* (> 1.08 m^2) sizes, based on the spread of points. Effects of kelp density, reef size group (small or large), and habitat position were then analysed using permutational multivariate analysis of variance (PERMANOVA). Where interactions of main effects occurred, attempts were made to remove the interaction by separately analysing subsets of reefs at different factor levels. Post-hoc tests were subsequently used to identify significant ($P < 0.05$) pairwise comparisons.

Regression analysis was used to explore the relationships between algal richness and richness of associated epifauna (standardised to the biomass of the algae). Multiple regression was used to investigate the influence of abiotic (relative light, water flow, sediment deposition and sediment accumulation) and biotic factors on total epifaunal secondary productivity. Biotic factors were measured as biomass density (dry weight as g m^{-2}) of all foliose algae (including *Ulva* sp.), *Ulva* sp. on its own, filamentous algae, corticated algae, leathery macrophytes, filamentous and corticated algae combined, all algae combined, and as percentage cover of sessile invertebrates.

Productivity of filter feeders and organisms which feed on both MPB and detritus (hereafter MPB/detritus feeders) were also assessed separately in order to investigate the role of feeding strategy in determining the production of the two most dominant groups of invertebrates. Only abiotic factors were investigated for RFH as algal habitat structure was assumed not to have a major effect on these samples, whilst both abiotic and biotic factors were investigated

for NH, separately and in combination. Normality, linearity and homogeneity of variance of response variables were investigated with a scatterplot matrix and diagnostic plots (as outlined for ANCOVA). Multi-collinearity was investigated through pairwise correlations and the variance inflation factor of predictor variables. Biotic predictor variables were all correlated to some degree and so not independent, and light was also highly correlated with the biomass of filamentous and branching corticated species. To address multi-collinearity, correlated terms were separately included in the multiple regression models, and the term resulting in the model with poorest explanatory power was then excluded from subsequent analyses. Model selection was achieved by comparing the fit of all possible models for each response variables (Quinn and Keough 2002) using AIC (Akaike's Information Criterion) and the *leaps* package. Hierarchical partitioning was also used to determine the independent contribution of each of the predictor variables considered in each multiple regression model using the *hier.part* function. We then determined the likelihood that the independent contribution could be due to chance by performing a randomization test and assessing the significance of the *Z* scores at the 95% confidence level.

4.4 Results

4.4.1 Secondary production: RFH

There was generally a negative relationship between kelp cover and secondary productivity of epifauna associated with rope fibre habitats (RFHs). Secondary productivity of epifauna associated with RFHs was significantly higher at the reef edge compared to the centre of the patch reefs (Fig. 4.1a, Table 4.1). For RFHs in both positions, epifaunal productivity increased significantly with decreasing patch size. However, the increase was greater with centrally positioned RFHs, with the smaller patches (< 0.48 m^2) supporting around 10 times

the productivity of the largest patch (7.68 m^2). Kelp density also had similar significant effects across the two habitat positions, with reefs from which kelp was absent supporting higher epifaunal productivity than the medium-kelp-density-reefs in both locations. However, in the patch centre only, reefs with no kelp also supported higher productivity of epifauna than both the medium-kelp-density-reefs and the high-kelp-density-reefs. On average RFHs situated in the centre of reefs without kelp supported epifaunal communities that were twice as productive as equivalent habitats on reefs with medium (i.e. density of nearby reefs) or high (double that on natural reefs) densities of kelp.

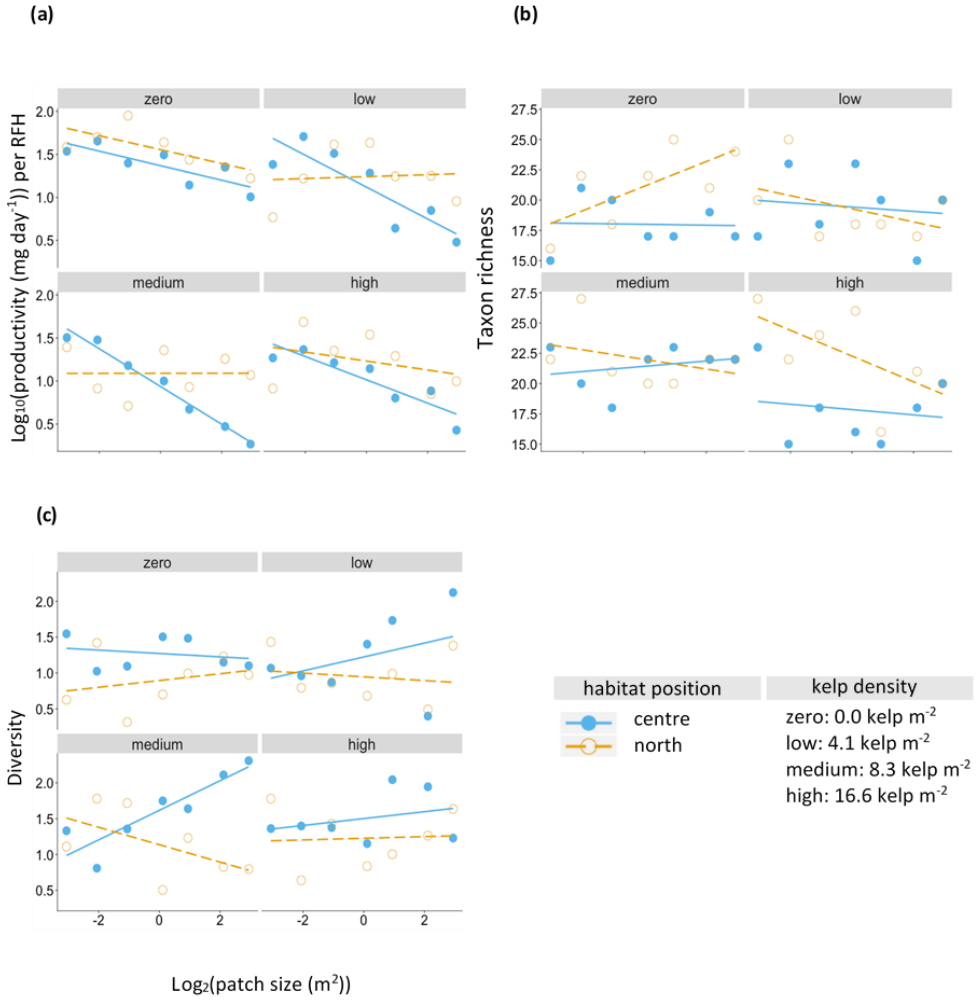

Figure 4.1a) Secondary productivity, b) epifaunal taxon richness, and c) Shannon-Weiner diversity index of epifauna associated with rope fiber habitats (RFH) positioned either on the northern edge or the center of reefs of different size and kelp density.

Model	factor	SS (df)	F-value	p-value	Post-hoc
RFH: CENTRE & NORTH					
Productivity $\log_{10}(Y)^{0.86}$	$\log_2$(patch-size)	1.46 (1, 47)	25.57	< 0.001 *	
	kelp density	0.55 (3, 47)	3.24	< 0.001 *	
	position	0.12 (1, 47)	2.12	0.030 *	N > C
Richness $(Y)^{0.77}$	$\log_2$(patch-size)	0.70 (1, 47)	0.59	0.446	
	kelp density	8.82 (3, 47)	2.49	0.072	
	position	10.17 (1, 47)	8.63	0.005 *	N > C
Diversity $(Y)^{1.06}$	$\log_2$(patch-size)	0.25 (1, 47)	1.21	0.277	
	kelp density	0.85 (3, 47)	1.38	0.261	
	position	0.30 (1, 47)	1.48	0.230	
RFH: CENTRE					
Productivity $\log_{10}(Y)^{1.11}$	$\log_2$(patch size)	3.43 (1, 23)	74.93	< 0.001 *	zero > medium, high
	kelp density	0.90 (3, 23)	6.56	0.002 *	
Richness $(Y)^{1.23}$	$\log_2$(patch-size)	2.38 (1, 23)	0.06	0.805	
	kelp density	340.62 (3, 23)	2.97	0.053	
Diversity $(Y)^{1.44}$	$\log_2$(patch size)	2.64 (1, 23)	5.92	0.023 *	
	kelp density	2.02 (3, 23)	1.51	0.248	
RFH: NORTH					
Productivity $\log_{10}(Y)^{1.31}$	$\log_2$(patch size)	0.24 (1, 23)	1.54	0.227	
	kelp density	1.64 (3, 23)	3.45	0.033 *	zero > medium
Richness $(Y)^{0.39}$	$\log_2$(patch size)	0.02 (1, 23)	0.60	0.448	
	kelp density	0.14 (2, 23)	1.35	0.284	
Diversity $(Y)^{0.61}$	$\log_2$(patch size)	0.01 (1, 23)	0.20	0.659	
	kelp density	0.19 (3, 23)	0.97	0.425	
NH					
Productivity $\log_{10}(Y)^{1.19}$	$\log_2$(patch size)	2.87 (1, 23)	42.52	< 0.001 *	
	kelp density	1.07 (3, 23)	5.29	0.006 *	high > low, medium
Richness $(Y)^{2.92}$	$\log_2$(patch size)	1.30e09 (1, 23)	50.99	< 0.001 *	
	kelp density	5.84e07 (3, 23)	0.76	0.527	
Diversity $(Y)^{3.87}$	$\log_2$(patch size)	914.42 (1, 23)	12.27	0.002 *	
	kelp density	573.03 (3, 23)	2.56	0.080	

Table 4.1. Summary of ANCOVA models testing the effects of kelp density, reef size and when relevant fibre habitat (RFH) position, on secondary productivity, taxon richness and Shannon-Weiner diversity index of epifauna associated with RFHs and natural algal habitat (NH). Model output is from the reduced models after confirming homogeneity of slopes. Response variable transformations are shown in the model column. The covariate reef size was $\log_2$ transformed. Significant P-values from the ANCOVA are denoted with *****. Significant post-hoc pairwise comparisons between habitats at the northern edge (N) and centre (C) of reefs and between reefs supporting different kelp densities are indicated in the Post-hoc column.

4.4.2 Secondary production: NH

There was a more complex relationship between kelp cover and productivity of epifauna within natural habitats (NH). Secondary productivity of epifauna associated with NH increased significantly with declining patch size (Fig 4.2a, Table 4.1). However, unlike the RFHs, epifaunal productivity associated with NH was significantly greater on reefs with a high kelp density than reefs supporting low and medium kelp densities and were similarly productive to reefs without kelp. On average reefs without kelp and kelp at high density supported epifaunal assemblages that were approximately twice as productive compared to the assemblages on reefs with intermediate (low and medium) kelp densities.

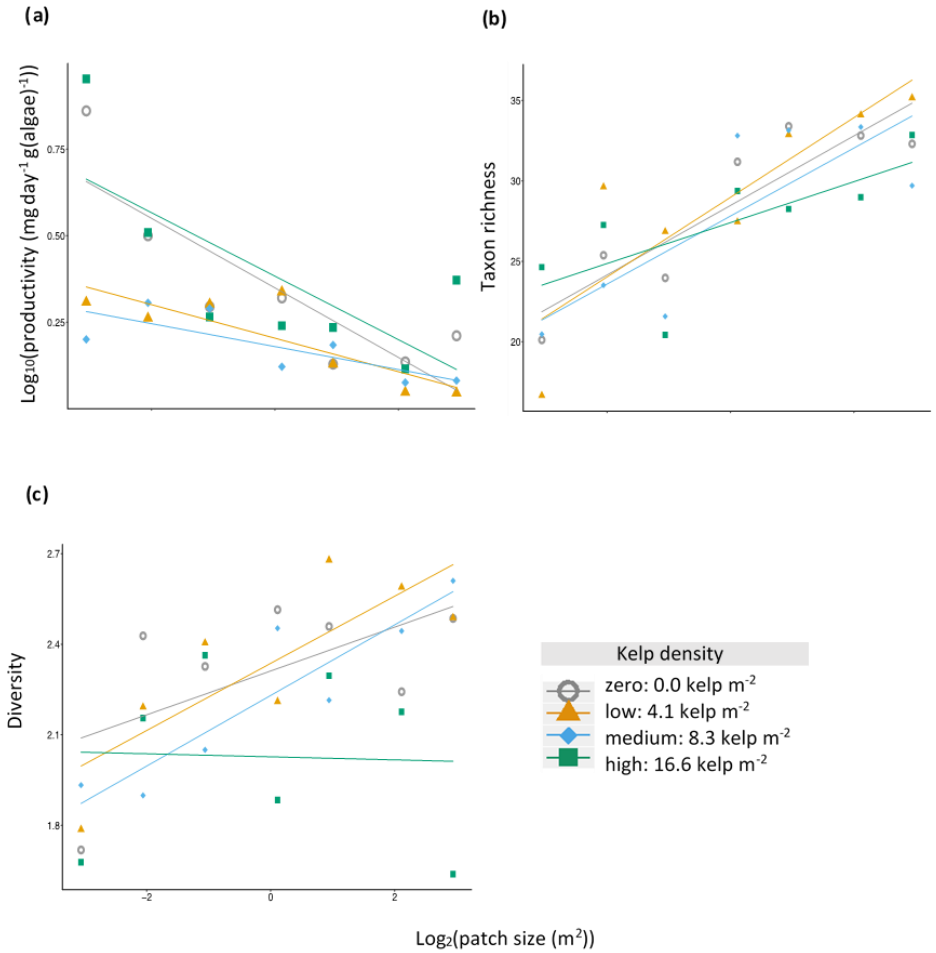

Figure 4.2 a) Secondary productivity, b) epifaunal taxon richness (standardized to algal biomass), and c) Shannon-Weiner diversity index of epifauna associated with natural algal habitat on reefs of different size and kelp density.

4.4.3 Taxonomic richness: RFH

Habitat position (edge *vs*. centre) was the main factor influencing taxonomic richness of epifauna associated with the RFHs. RFHs supported between 15 and 28 taxa of epifauna. Overall, taxonomic richness was significantly higher at the edge of reefs compared to the centre, and reef size had no effect on richness in either habitat position (Fig. 4.1b, Table 4.1). Kelp density had a marginally non-significant ($0.05 < P < 0.1$) effect on richness of epifauna, that was not linear. The effect of habitat position on epifaunal richness was particularly pronounced on large patch sizes (> 1.08 m^2) without kelp and small patch sizes (≤ 1.08 m^2) supporting high densities of kelp, where edge habitats supported 5 – 10 more taxa than centre habitats.

4.4.4 Taxonomic richness: NH

Reef size had a major effect on the taxonomic richness of epifauna in NH. Richness of epifauna (standardised to algal biomass) associated with NH ranged from approximately 18 – 36 taxa. Epifaunal richness decreased significantly with declining patch size for all kelp densities, with reduction of approximately 50% moving from the largest to the smallest reefs (Fig. 4.2b, Table 4.1). No significant effects of kelp density were evident. Algal species richness and epifaunal richness were positively correlated ($r^2 = 0.69$, Fig. 4.3).

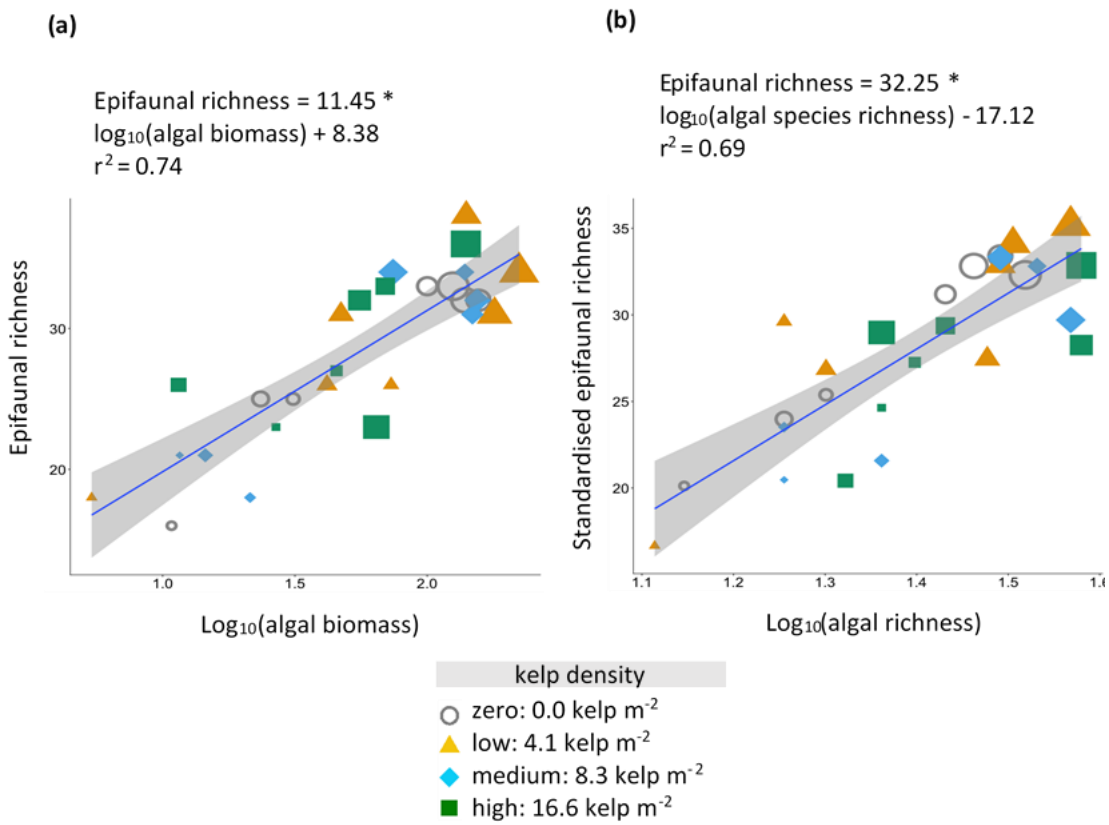

Figure 4.3. Relationships between a) epifaunal taxon richness and algal biomass and, b) epifaunal taxon richness standardized to algal biomass and algal species richness associated with natural habits (NH) on reefs of different size and kelp density. Shading shows 95% confidence intervals. The relative size of symbols reflects the size of patches.

4.4.5 Diversity: RFH

Reef size influenced the diversity of epifaunal assemblages on centrally positioned RHFs only. Diversity of epifauna decreased significantly with declining reef size for RFH in the patch centre, but was not affected by patch size at the reef edge (Fig. 4.1c, Table 4.1). Kelp density did not have a significant effect in either position. However, the decline in diversity with reductions in reef size in centre positions was most pronounced on reefs supporting medium kelp densities, where there was an approximate two-fold difference in invertebrate diversity between the largest reef sizes and the smallest reef sizes.

4.4.6 Diversity: NH

Reef size also influenced diversity of epifaunal assemblages in NH. Diversity of epifauna associated with NH decreased significantly with declining reef size, whilst effects of kelp density on epifaunal diversity was marginally non-significant ($P = 0.08$) (Fig. 4.2c, Table 4.1). With the exception of reefs supporting high densities of kelp, there was an approximate 20% reduction in diversity moving from the largest reef size to the smallest.

4.4.7 Community structure: RFH

A lack of kelp cover led to more homogeneous epifaunal assemblages on RFHs. The MDS depicting the community structure of epifauna associated with RFHs shows that small reefs (Fig. 4.4a), reefs without kelp (Fig. 4.4b), and habitats positioned at the edge of reefs (Fig. 4.4c) supported relatively homogenous assemblages, compared to assemblages associated with larger reefs, those with kelp, and those positioned at the reef centre, which were more variable. The associated PERMANOVA for all RFHs showed a significant reef size group x habitat position effect on epifaunal community structure (Appendix B: Table B. 2). Separately assessing the communities associated with small (≤ 1.08 m^2) and large (> 1.08 m^2) reefs (to remove the effect of the interaction), revealed that kelp density only had a significant effect on large reefs, whilst habitat position had significant effects for both reef size groups. Epifaunal communities on large reefs without kelp were distinct from all other kelp density treatments (Fig. 4.4b). For centrally positioned habitats, there was a significant reef size group x kelp density interaction (Fig. 4.4a, 4.4b), whilst for habitats positioned at the reef edge, small reefs were distinct from large reefs (Fig. 4.4a). The CAP maximising separation across kelp density categories did not indicate distinct clustering of epifaunal communities associated with RFHs in the centre of patches (Appendix B: Fig. B. 2).

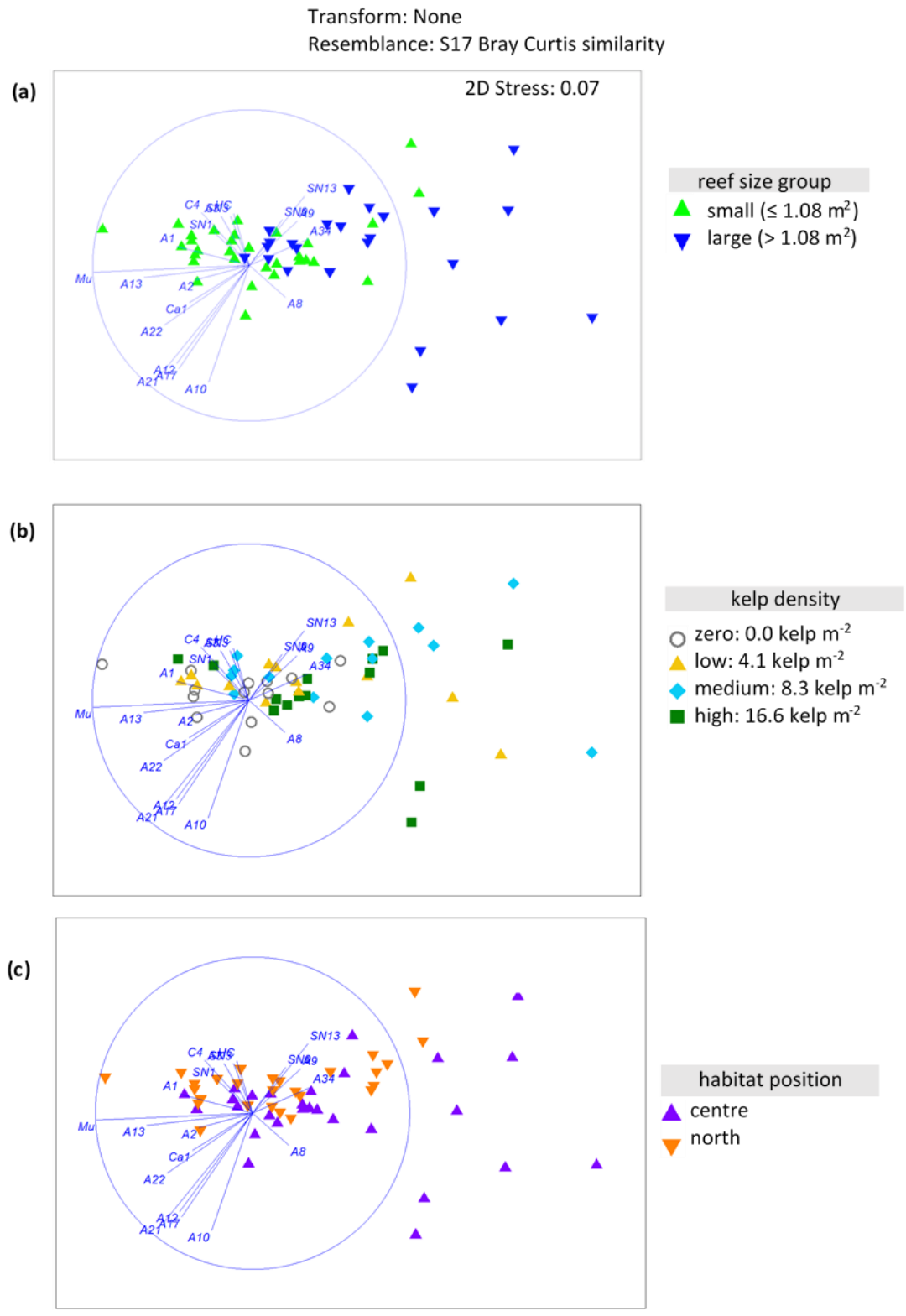

Figure 4.4. MDS of epifaunal invertebrate communities associated with rope fibre habitats, separately labelled to indicate a) patch size, b) kelp density, and c) habitat position effects. Vector overlay depicts species with Spearman correlations > 0.3. Refer to Appendix B: Table B. 1 for taxon ID.

4.4.8 Community structure: NH

Kelp cover also affected the community structure of epifauna within NH. However, in contrast to RFHs, MDS for NH revealed greater variability in epifaunal communities between reefs that were small in size and which supported no kelp (Fig. 4.5a, 4.5b). However, the communities still differed significantly with patch size and kelp density (Appendix B: Table B. 2). As per the results for the RFH in the patch centre, epifaunal community structure on reefs without kelp differed significantly from the community structure on reefs with low, medium and high kelp densities of kelp, but additionally the communities on low-kelp-density-reefs also differed from the communities on high-kelp-density-reefs. These results were supported by the CAP, which also separated samples from low- and high-density kelp (Appendix B: Fig. B. 2).

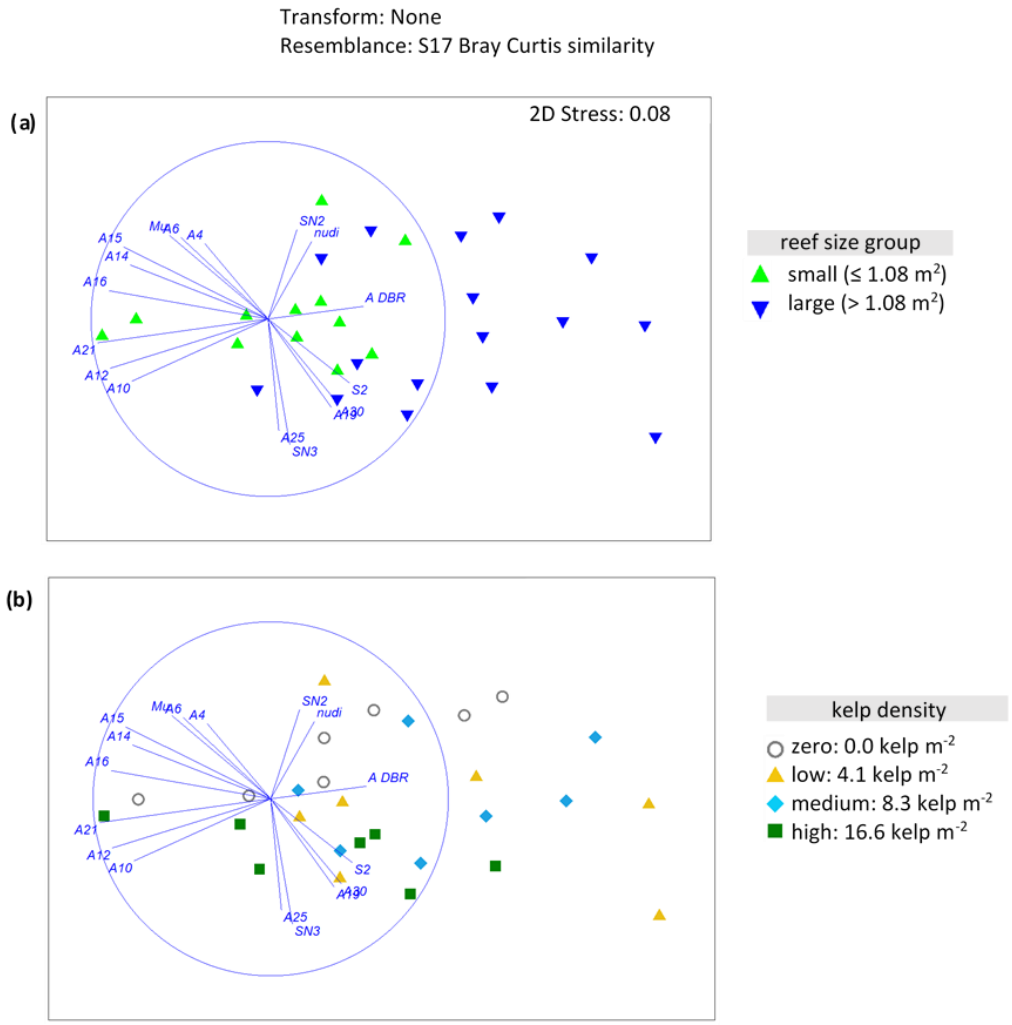

Figure 4.5. MDS of epifaunal invertebrate species associated with natural algal habitat, separately labelled to indicate: a) patch size, and b) kelp density effects. Vector overlay depicts species with Spearman correlations > 0.5. Refer to Appendix B: Table B. 1 for taxon ID.

4.4.9 Abiotic drivers: RFH

Light (positive effect) was the single most important abiotic factor explaining variability in secondary productivity of epifauna on RFHs. The best abiotic predictors of total epifaunal secondary productivity on (centre) RFHs were: sub-canopy light, water flow, and benthic sediment accumulation (all positive effect), although only light was significant in the multiple regression model with these factors (Appendix B: Table B. 3). In combination, these three factors explained 76% of the variability in secondary productivity, however only light (49%)

and sediment accumulation (25%) had significant independent contributions in the hierarchical partitioning. Abiotic factors explained much more of the variability in secondary productivity associated with filter feeders (79%) than MPB/detritus feeders (46%), with light having the dominant influence on both feeding strategies.

4.4.10 Abiotic and biotic drivers: NH

Sub-canopy light (positive effect), water flow (positive effect) and the biomass of *Ulva* sp., (negative effect) were consistently identified as important factors explaining variability in epifaunal productivity in NH. Abiotic factors explained less of the variability in epifaunal productivity in NH compared to RFHs (total = 50%; filter feeders = 65%; MPB/detritus = 46%) (Appendix B: Table B. 3). For all abiotic models, light and flow were consistently identified as important factors. The best biotic predictor of secondary productivity for all groups of epifauna was the biomass of *Ulva*, which explained a similar proportion of the variability in secondary productivity for different epifaunal groups (total = 59%; filter feeders =63%; mixed feeders = 49%) as abiotic factors. The optimal models containing both abiotic and biotic factors for all epifaunal groups always included *Ulva* biomass and water flow. For filter feeders, light and sediment accumulation (positive effect) were additionally important. Combined (abiotic and biotic) models explained 66%, 76% and 57% of variability in secondary productivity for all epifauna, filter feeders, and mixed feeders respectively.

4.4.11 Feeding strategies: RFH & NH

We found no evidence that feeding strategy influenced the response of epifauna to *E. radiata* patch size or density. By far the predominant feeding strategies present amongst epifauna associated with (centre) RFH (Appendix B: Fig. B. 3a), and those present amongst NH (Appendix B: Fig. B. 3b), were filter feeders (primarily bivalves) and species that feed on a

mixture of MPB and detritus (MPB/detritus feeders, mainly amphipods). However, with RFHs, filter feeders were much more dominant than MPB/detritus feeders (~ 70% vs. 20% respectively), whilst the relative dominance of these groups was reversed with the NH (~ 20% vs. 60%). The productivity of both groups showed highly similar effects of patch size and kelp density when the sampling methodology (RFH or NH) was consistent (Fig. 4.6) and the productivity of both groups resembled the patterns of total secondary productivity of the community previously described (Figs. 4.1a, 4.2a).

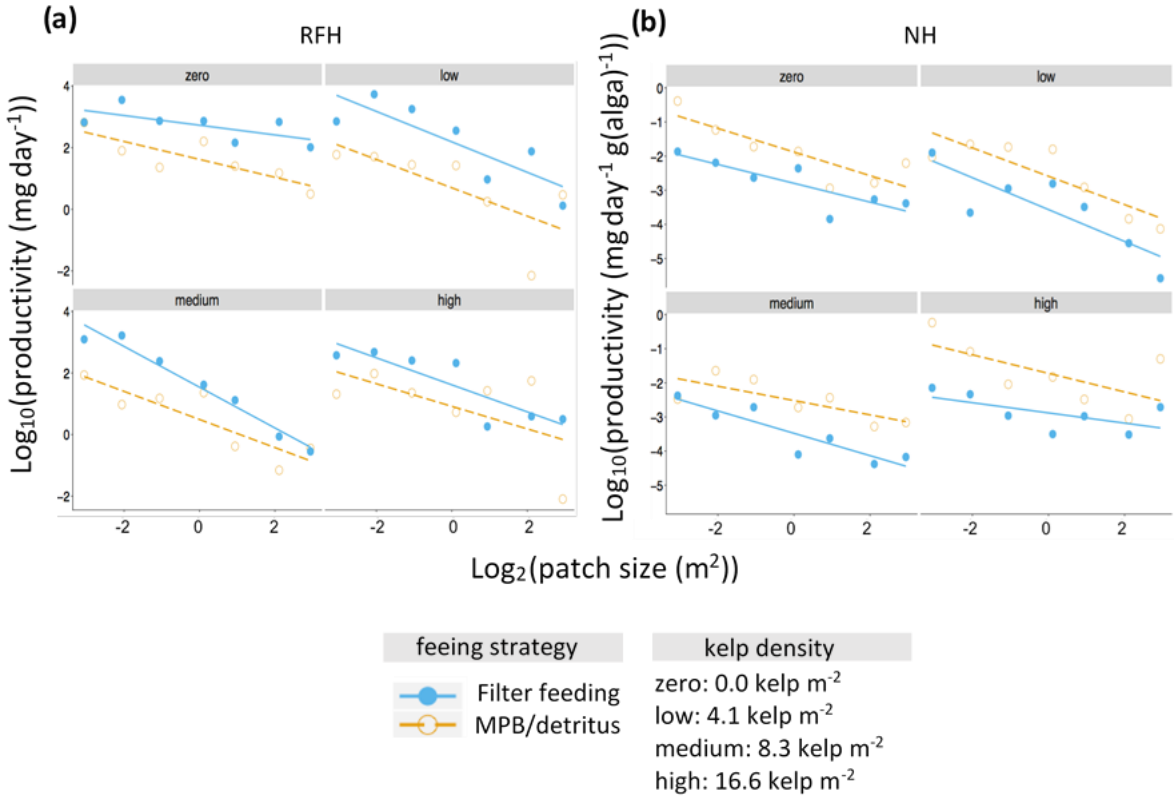

Figure 4.6. Secondary productivity of Microphytobenthic (MPB)/detritus feeding epifauna and filter feeding epifauna associated with a) RFH and b) natural algal habitat (NH), from reefs of different patch size and density. RFHs were positioned in the centre of reefs.

4.5 Discussion

Consistent with many macrophyte dominated ecosystems (i.e. seagrass and macroalgae), epifaunal assemblages on the reefs consisted mainly of small mobile grazers such as

amphipods (Edgar 1990a), which tend to reach successional maturity and a carrying capacity within 2-4 months (Edgar 1991a). *Ecklonia radiata* had a moderating effect on the productivity of epifauna at the benthos, with increases in epifaunal productivity evident with declining *E. radiata* patch size and elevated secondary productivity in the absence of an *E. radiata* canopy. However, in natural algal habitat (NH) only, secondary productivity was also elevated on reefs supporting high densities of kelp (Fig. 4.7). Biodiversity, in terms of both epifaunal taxon richness and diversity, declined with patch size, but was not affected by kelp density. However, the community structure of epifauna on reefs without kelp differed from those on reefs with kelp. Overall, secondary productivity of epifauna appeared to be positively associated with higher sub-canopy light and water flow as kelp patch size and density decreased and negatively associated with the biomass of the most abundant species of understory algae, i.e. *Ulva* sp. (Fig. 4.7).

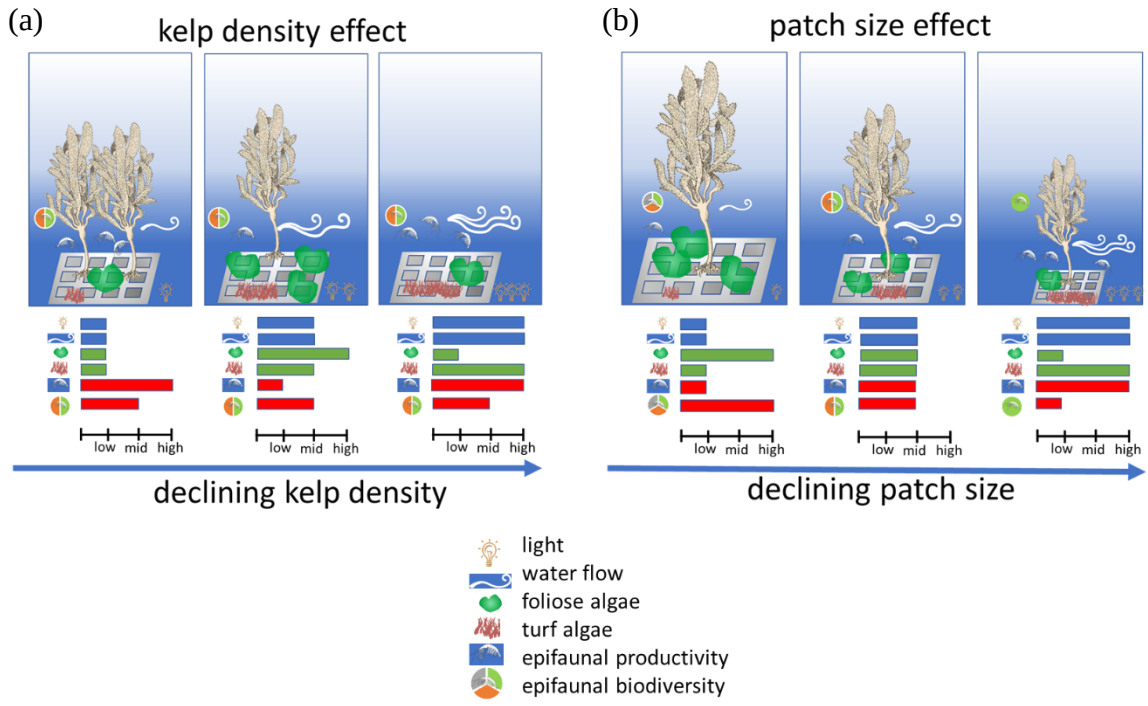

Figure 4.7. Summary of major effects of declining a) kelp density and b) patch size on understory epifaunal assemblages associated with natural algal habitat and corresponding changes in influential abiotic and biotic factors. Horizontal bars indicate relative strength of abiotic influences (light and water flow, blue bars), biotic influences (foliose and turf algae, green bars), and epifaunal responses (productivity and biodiversity (as both richness and diversity), red bars).

4.5.1 Secondary productivity

We demonstrate that differences in kelp patch size and density and edge effects are likely to affect secondary productivity of benthic epifauna in *E. radiata* kelp forests. Secondary productivity of invertebrate epifauna increased with declines in artificial reef size and was higher at the edge of reefs compared to the centre for rope fibre habitats (RFHs) (Figs. 4.1a, 4.2a, Table 4.1). Reefs without kelp also had higher epifaunal productivity than reefs with kelp, but an important exception occurred within NH, where reefs supporting the highest density of kelp had similarly high epifaunal productivity to the reefs with no kelp (Fig. 4.2a). As RFHs did not show this response, structural changes to benthic algae will likely contribute to changes in epifaunal productivity resulting from loss of kelp, in addition to abiotic changes. We found no evidence that feeding strategy (filter feeder vs. MPB/detritus) affected the productivity of epifauna.

The observed variability in epifaunal productivity in our experiment is largely consistent with previous research conducted in Australia and New Zealand that investigate the effects of macrophyte (macroalgae and seagrass) patch size (Roberts and Poore 2006), presence *vs*. absence of vegetation (Taylor 1998) and edge effects (Bologna and Heck 2002), but with some notable exceptions. Consistent with our results, Roberts and Poore (2006) found an increase in epifaunal abundance with reductions in patch size for isolated patches of *Sargassum linearifolium* on sand, whilst conversely, Bell et al. (2001) observed no effect of patch size on epifauna within a comparatively connected seagrass habitat. These findings suggest that landscape context (i.e. levels of connectivity between habitat patches) and/or macrophyte identity may mediate the impact of patch size on epifauna. The observed increase in epifaunal productivity at the edge of *E. radiata* patches is supported by studies within

seagrass ecosystems, and indicates that macrophyte edges likely provide an important trophic conduit for fish and macro-invertebrates that feed on epifauna within fragmented habitats (Bologna and Heck 2002, Macreadie et al. 2010). Also consistent with our findings, Taylor (1998) recorded lower secondary productivity on rocky reef with canopy-forming kelp compared to reef without a canopy of kelp but still covered with benthic algae. However, when kelp forest is replaced by a barren landscape that is devoid of benthic algae (e.g. due to over-grazing by sea urchins), there is likely to be a loss epifaunal productivity and biodiversity (Ling 2008). Similarly, the loss of seagrass from sandy substratum results in an overall loss of small invertebrate grazers (Edgar 1990a, Connolly 1997). Thus, while the physical structure provided by benthic algae and seagrass is critical in supporting the presence of small mobile invertebrates, canopy-forming species can clearly mediate associated levels of secondary productivity.

Our results also support the notion that the composition of sub-canopy algae on rocky reef influences epifaunal productivity. Although the proliferation of algal turfs (which often is concomitant with loss of kelp cover) sometimes leads to reduced productivity of epifauna on a per unit area basis (Miller et al. 2009), our results and other studies (Miller et al. 2009, Lavender et al. 2017) indicate that turfs (which were dominant on the reefs without kelp) are likely to support extremely productive communities of epifauna per unit of algal biomass. In contrast to results by Miller et al. (2009), we also found that turfs on the reefs without kelp also supported high secondary productivity per unit area (Appendix B: Fig. B.4). Consequently, the replacement of kelp forest by algal turfs could result in elevated food resource availability for higher trophic level consumers.

4.5.2 Community responses

The observed decrease in epifaunal richness with declines in patch size corresponded with a loss of sub-canopy-algal richness. The strong correlation between algal species richness and epifaunal richness in NH (Fig. 4.3b) is consistent with the idea that greater variety of food, refuges and other resources provided by the different algal species leads to richer faunal assemblages (Edgar 1990a). Richer algal assemblages are also likely to generate more diverse sources of primary production, which could lead to increased resource partitioning resulting in richer faunal assemblages (Bruno et al. 2005). Although contrary to the findings of Bates and DeWreede (2007), the positive effect of algal richness on epifaunal richness highlights the importance of species rich assemblages of habitat-forming species in supporting biodiverse ecosystems. However, it is unclear whether broad-scale kelp habitat degradation will necessarily have a negative impact on the richness of benthic algal assemblages. The loss of epifaunal richness with diminishing patch size in NH was probably influenced by the different area of reef being sampled. Curiously, epifaunal taxon richness was greater at the reef edge compared to the centre (Fig. 4.1b, Table 4.1), indicating that some species preferred the ecotonal edge environments and avoided the patch interior. Alternatively, patch-edge micro-habitats may experience a level of disturbance from abiotic factors or predation that maximises biodiversity (i.e. consistent with the intermediate disturbance hypothesis (Connell 1978)).

Both sampling methodologies showed significant differences between epifaunal communities on small and large reefs, and on reefs with and without kelp (Figs. 4.4, 4.5; Table 4.1), indicating that kelp loss and patch size reduction will transform epifaunal communities. Furthermore, the decline in epifaunal diversity that occurred with reducing patch size for both NH and centrally positioned RFHs (Fig. 4.1c, 4.2c; Table 4.1), supports the notion that kelp habitat loss is likely to have a negative influence on biodiversity (Graham 2004). There were

also different epifaunal assemblages associated with RFHs at the reef edge compared to the centre of patches (Fig. 4.4c; Appendix B: Table B. 2), and differences in assemblages occurring within NH on low-kelp-density reefs compared to high-kelp-density reefs (Fig. 4.5b; Appendix B: Table B. 2). These results additionally indicate that community structure is susceptible to change with kelp habitat fragmentation and declines in density.

RFHs on all reefs < 2 m^2 supported similar epifaunal communities, regardless of kelp presence or edge effects (Fig. 4.4; Appendix B: Table B. 2). This could suggest that when patch size erodes to < 2 m^2, abiotic ecosystem engineering by kelp ceases to have a meaningful influence on epifauna community development. In contrast, there was greater variability in epifaunal communities within NH on small reefs, and reefs without kelp tended to manifest different communities to reefs with kelp for all reef sizes (Fig. 4.5; Appendix B: Table B. 2). Therefore, variability in the biotic environment (i.e. the composition of understory algae) may continue to influence epifaunal communities, even after significant degradation and loss of patch size.

4.5.3 Biotic drivers

The biomass of the most dominant foliose algal species *Ulva* sp. was the major factor (abiotic and biotic) negatively associated with total secondary productivity of epifauna and the productivity of both MPB/detritivores and filter feeders (Appendix B: Table B. 3). Similar to kelp, a sub-canopy of *Ulva* may modify the abiotic and biotic benthic environment and thus influence epifaunal secondary productivity. Shading by *Ulva* could reduce micro-and-macro-algal growth, while it's structure could obstruct water flow, negatively impacting the delivery of suspended resource subsides (Eckman et al. 1989). Additionally, it's broad foliose thallus may affect the density and foraging efficiency of predators (Wilson et al. 1990), which may

influence epifaunal colonisation (Duffy and Hay 1991), although foliose species typically provide less refuge for small epifauna than highly branched species (Hacker and Steneck 1990, Bates and DeWreede 2007).

The size distribution of epifauna, and hence productivity:biomass (P:B) ratio, can be indicative of predation pressure (Edgar and Aoki 1993). Therefore, the fact that epifaunal P:B within NH increased significantly with loss of patch size, whilst it decreased for RFHs at the reef edge and was unaffected by reef size in the centre of reefs (Appendix B: Fig. B. 5, Table B.3), indicates that understory algal structure may have impacted predation rates by fish or invertebrate predators in this study. Although predation may influence choice of algal habitat by epifauna, it won't necessarily impact epifaunal productivity due to the rapid regeneration time of many species (Edgar and Aoki 1993). Therefore, differences in the abundance and composition of fish and macroinvertebrate predators associated with our artificial reefs compared to natural reefs are unlikely to affect broad patterns in epifaunal productivity. Few epiphytic algae were observed on *Ulva*, reducing the potential for high secondary productivity (Johnson and Scheibling 1987). Given the tremendous dominance of *Ulva* and similar foliose species in coastal waters, and their tendency to be associated with ephemeral blooms (Fletcher 1996), understanding the relationship between this species and secondary productivity should be prioritised in future research. *Ulva* tended to be most prevalent on larger reefs with low and medium kelp densities (Appendix B: Fig. B. 6), which could indicate that declines in *E. radiata* density are likely to facilitate an increased dominance of this species, and less productive food webs overall.

4.5.4 Abiotic drivers

Our results are consistent with the notion that secondary productivity is constrained by quantifiable resource ceilings governed predominantly by the availability of light (Edgar and Aoki 1993), with a positive correlation between light and productivity of all epifauna, MPB/detritus feeders and filter feeders in NH and centre RFHs. However, we did not separate the effects of light availability from algal species composition. Benthic light availability is likely to have directly influenced resource availability for MPB/detritus feeding epifauna and herbivores by influencing growth of MPB and epiphytic algae but is unlikely to have directly affected food resource availability for filter feeders. The positive correlation between light and productivity of filter feeders may result from variability in larval settlement, however, a majority of benthic invertebrates have a negative response to light during settlement (Thorson 1964). Alternatively, post-settlement mortality could have been negatively correlated with light, although this is contrary to findings by Miller and Etter (2008).

Other abiotic factors including water flow and sediment accumulation appeared to have positive effects on productivity of epifauna across the artificial reefs (Appendix B: Table B. 3). Flow is likely to be an important factor in the delivery and uptake of food by filter feeders (Lenihan et al. 1996). The mechanism whereby flow influences MPB/detritus feeding invertebrate functional groups is not clear, but possibly relates to nutrient delivery affected by boundary layer formation. Some invertebrates, especially filter feeders, may also seek out high flow areas during or after settlement (Dobretsov and Wahl 2008). Thus, productivity of epifauna may have been positively associated with particle accumulation rates as this metric partially reflects the quantity of planktonic resource subsidies deposited to the benthos or it could relate to (passive) larval settlement rates. Although we identified several factors which are likely to influence secondary productivity, the potential contribution of other factors

(including factors weakly and non-significantly associated with secondary productivity here) cannot be discounted without further investigation.

4.5.5 Temporal effects

Secondary productivity and community structure of epifaunal assemblages often vary temporally, with incremental increases in species richness and abundance occurring through the colonisation of new habitat (Edgar 1991a), as well as substantial seasonal fluctuation in productivity (due to changes in water temperature and epiphytic algal growth) (Edgar 1990b). The patterns in epifaunal productivity and biodiversity (with respect to *E. radiata* patch size and density) that we observed are likely to be indicative of responses of 'mature' epifaunal communities. Abiotic and biotic ecosystem engineering by canopy-forming kelp is therefore likely to persist year-round. However, epifaunal productivity will increase with seasonal warming and increases in epiphytic algal growth (Edgar 1983b, Edgar 1990b). Seasonal, successional and stochastic changes in understory algal assemblages are also likely to influence the composition and productivity of epifauna (Dean and Connell 1987). Regardless, the dominance of the major algal functional groups appeared to stabilize in our study after approximately six months following the initial transplantation of *E. radiata* (Shelamoff et al. unpublished manuscript), with little subsequent change at 12 months (for RFHs) and 24 months (for NH).

4.5.6 Future trajectories under degradation

Interactions between kelp–, foliose algae–, turf algae –and epifauna profoundly affect the productivity and biodiversity of temperate reefs. A loss of *E. radiata* and reduction in patch size will likely lead to increased abundance of algal turfs, whilst a decline in *E. radiata* density can lead to increased prevalence of foliose species (Flukes et al. 2014, Filbee-Dexter

and Wernberg 2018). Areas dominated by algal turfs are likely to support elevated epifaunal productivity (Lavender et al. 2017), but will likely lack diverse structural refuges needed to attract and support diverse assemblages of larger invertebrates and fishes (Filbee-Dexter and Wernberg 2018). In contrast, a dominance of foliose species such as *Ulva* sp. may result in low secondary productivity of epifauna, but can potentially provide a refuge for larger fauna (Wilson et al. 1990). Temporal variability in the biomass of turfs and foliose algae influenced by stochastic and seasonal events, are likely to have significant implications for epifaunal assemblages and ecosystem function. The complex tradeoffs and synergies between diversity and productivity of epifaunal assemblages associated with degradation to kelp habitat, including interaction with other macroalgae, clearly warrant further investigation.

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Chapter 5. High kelp density attracts fishes other than recruiting cryptobenthic species

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5.1 Abstract

As foundation species, kelp support productive and species rich communities; however, the effects of kelp structure on mobile species within these highly complex natural systems are often difficult to assess. We used an experimental array of artificial reefs with transplanted kelp to quantify the influence of kelp patch size and density on fish assemblages and the arrival of recruiting cryptobenthic species. Large patches with dense kelp attracted the highest abundance, species richness, and diversity of fishes, whilst the abundance of recruits in artificial collectors declined with patch size and was lowest on reefs with sparse kelp compared to reefs with dense kelp or no kelp. These results highlight the importance of dense kelp cover in facilitating biodiversity and indicate that coastal ecosystems are likely to benefit from establishing kelp on natural and artificial structures. Kelp also apparently drives complex interactions affecting the recruitment/behaviour of some cryptobenthic species.

5.2 Introduction

Habitat-forming foundation species are disproportionately important to the productivity and biodiversity of coastal ecosystems in temperate and tropical waters. Habitat-formers such as corals, shellfish, seagrass, mangroves, and macroalgae provide complex physical structure that ameliorates environmental stress, augments the supply of food and shelter, and manifests a variety of microhabitats which helps support species rich assemblages including many fishes (Coker et al. 2014, Norling et al. 2015, Serrano et al. 2017, Teagle et al. 2017). Foundation species also drive trophic and competitive interactions which can further influence community dynamics (Graham 2004, Bonin et al. 2009). Many foundation species are also integral to the replenishment of populations by providing cues for larval settlement

and increasing post-settlement survival prospects (Ermgassen et al. 2016, Whitfield 2017). Variability in the structural configuration of habitat-formers, in terms of their patch size and density will affect how these species influence the associated communities.

Canopy-forming macroalgae of the orders Laminariales and Fucales (hereafter collectively referred to as *kelp* (Fraser 2012)) are the dominant habitat-forming species in temperate and subpolar coastal waters, where they can generate forests which support many associated fish species. Kelp forests often form patchy habitat mosaics where the size of patches and the density of kelp within patches is variable in both space and time (Dayton 1985b). Furthermore, in many areas increased environmental stressors (e.g. ocean warming, changed ocean currents, increased herbivory, over-harvesting, coastal modification) are degrading these systems, resulting in kelp loss, increased habitat fragmentation and reductions in kelp patch size and density (Ling et al. 2009a, Johnson et al. 2011, Krumhansl et al. 2016). Despite widespread acknowledgement of the importance of kelp structure on community dynamics, the consequences of variability in kelp patch size and density on fish communities, and the recruitment of many species, is unclear (Villegas et al. 2008, Bertocci et al. 2015).

The effects of *Macrocystis pyrifera* structure on fish communities and recruitment have been well documented in California, USA (Carr 1989, Anderson 1994, Deza and Anderson 2010, Miller et al. 2018) while several other studies examine the role of other kelp species elsewhere (Levin and Hay 1996, Metzger et al. 2019, Srednick and Steele 2019). However, comparatively scant experimental work has investigated the separate and combined effects of patch size and density of kelp species other than *M. pyrifera* on fish assemblages which uniquely extends 10s of metres into the water column (Bertocci et al. 2015). Furthermore, few studies looking at patch size and density have been conducted at scales (approximately 1

- 10m^2) that are relevant for understanding effects of microhabitat variability, threshold habitat requirements, or severe habitat decline.

Although increases in kelp patch size and density may enhance the biomass, species richness and diversity of fishes (DeMartini and Roberts 1990, Deza and Anderson 2010), loss or decline in kelp cover can sometimes have relatively little effect on fish assemblages (Halpern and Cottenie 2007), especially if the scale of loss is small and the surrounding forest remains intact (Edgar et al. 2004). Kelp structure may influence the associated communities directly by modifying the provision of food (including detrital subsides), as well as the availability and/or quality of refuge (Graham 2004, Teagle et al. 2017). Furthermore, kelp structure can also affect assemblages indirectly by modifying the composition and/or behaviour of other influential species such as predators or species that provide additional refuge (Efird and Konar 2014, O'Brien et al. 2018). For example kelp canopy density can affect the abundance of understory foliose algae (Flukes et al. 2014, Shelamoff et al. 2019), which can provide additional shelter for adult and juvenile fishes (Levin 1993, Efird and Konar 2014). Kelp also inhibits the growth of low-growing filamentous algal turfs, which can otherwise outcompete other algae that provide more structurally complex habitat (Filbee-Dexter and Wernberg 2018). However, turfs can also support a high abundance of small epifaunal invertebrates (Shelamoff et al. 2020), which are a dominant food source that supports many coastal fish species (Edgar and Shaw 1995a). Thus, there may be both positive (e.g. increased refuge) and negative (e.g. reduced food availability) effects of kelp structure on fish populations, although, responses are likely vary across species (Siddon et al. 2008, Cole et al. 2012).

Small cryptic fishes are diverse and abundant on coastal reefs and pivotal to trophic interactions in these ecosystems (Jones 1988, Brandl et al. 2019, Riginos and Leis 2019).

Many of these species may rely on kelp associated cues for settlement (Montgomery et al. 2001). Kelp fronds can also enhance post-settlement survival of recruits by providing food and refuge and by reducing the effect of predators (Connell and Jones 1991, Levin 1994b, Hunt et al. 2011). Kelp has been shown to positively influence the recruitment of some species (Levin and Hay 1996, McDermott and Shima 2006, Siddon et al. 2008, White and Caselle 2008) and negatively influences others (Levin 1993). The influence of habitat structure on setter mortality and recruitment may also be density-dependant i.e. the abundance of settlers arriving to area can mediate effects of predation and competition on recruitment (Hixon and Jones 2005). Recruitment of kelp-associated species is often complex and does not necessarily increase linearly with kelp patch size or density (Carr 1994, Steele et al. 2002, Deza and Anderson 2010). There are also numerous cryptic species, which commonly occur on rocky reefs for which the importance of kelp structure on recruitment is unknown (Willis and Anderson 2003, Pita et al. 2018).

To combat the decline of kelp forests and the impact on the associated communities, there is increasing effort to restore/supplement lost or degraded kelp habitat (Wood et al. 2019, Layton et al. 2020b). In some areas, where the coastline has been heavily modified, artificial reefs and other coastal infrastructure may be needed to provide substratum onto which kelp can be grown (Reed et al. 2006, Morris et al. 2019). The influence of kelp structure on fish assemblages is not only likely to influence how fishes respond to kelp habitat degradation, but it is also likely to impact the effectiveness of (re-)establishing kelp in coastal areas to support or aid the recovery of the associated communities. Establishment of fish assemblages could subsequently provide a positive feedback that supports kelp by directly and indirectly reducing the influence of grazing invertebrates (Pérez-Matus and Shima 2010). These fishes are also likely to contribute to community dynamics and trophic interactions more broadly,

and they may support recreational and commercial fisheries (Paxton et al. 2020). Enhancement of the communities and ecosystem services associated with the coastal zone is particularly crucial given heightened effects of environmental change on these ecosystems and their potential role in mitigation of some of these effects (Morris et al. 2018, Morris et al. 2019).

To better understand the role of kelp structure in influencing fish assemblages we used an array of artificial reefs with transplanted kelp to experimentally determine the effects of kelp patch size and density (across a habitat matrix with uniform but low levels of connectivity between patches) on 1) the abundance, biodiversity and composition of the associated fish assemblages, and 2) the arrival of common cryptobenthic fishes during their recruitment. This approach allowed us to make accurate manipulations in habitat structure whilst keeping other factors which might otherwise be highly variable on natural rocky reef and influence recruitment (e.g. topography and the surrounding habitat matrix) relatively constant. Although artificial structures may support different assemblages of fishes compared to natural rocky reefs, we would expect that the processes shaping population and community responses to kelp patch size and density would remain similar, however the net-outcome would additionally be shaped by other factors (such as connectivity to other habitat patches). We hypothesised that the abundance and biodiversity of fish assemblages and the abundance of recruiting cryptobenthic species would increase with kelp patch size and density.

5.3 Methods

5.3.1 Experimental system

Ecklonia radiata is the dominant species of canopy-forming kelp across Australasia and is the foundation species for biodiverse and productive reef communities (Bennett et al. 2016). It typically grows up to 1.5 m tall and can form subtidal forests down to depths of > 60 m. Similar to other kelp species globally, *E. radiata* forests are subject to escalating environmental stressors, which in Australia are causing this species to become sparser and more patchily distributed in some locations (Connell et al. 2008, Ling et al. 2009a, Johnson et al. 2011, Vergés et al. 2016, Wernberg et al. 2016, Reeves et al. 2018).

This research was conducted on the western side of Maria island on the east coast of Tasmania, Australia (-42.64693, 148.01481) and utilised an array of 28 artificial reefs. The reefs represented seven different patch sizes (0.12, 0.24, 0.48, 1.08, 1.92, 4.32 and 7.68 m^2), fully crossed with four densities of *E. radiata* (zero (0), low (4.1), medium (8.3) and high (16.6 kelp m^{-2}), fully described in Layton et al. (2019b). The medium density was equivalent to the mean density of *E. radiata* on rocky reefs in the region (i.e. 8 kelp m^{-2}). The reefs were constructed of concrete pavers elevated 0.3 m above the substratum on a steel frame (Fig. 5.1a) on an otherwise uniform sandy substratum at a depth of 6.5 m and were situated approximately 1.5 km from the nearest natural reef. The reefs were arranged in an approximate square grid with 25 m separating reefs. The infrastructure was deployed in December 2014 and adult *E. radiata* was first transplanted to the reefs in January and February 2015. Sampling of the associated (post-recruit, hereafter *adult*) fish communities took place from November 2015 to December 2016, whilst sampling of recruits took place from November 2015 to April 2016 (spanning the recruitment period for a majority of local species). Throughout the deployment of the experimental reefs, densities of *E. radiata* were maintained by replacing any losses with fresh transplants at regular intervals (approximately every six weeks), while communities of other algae, fishes and invertebrates proceeded to

establish naturally on the reefs (i.e. the addition of kelp was the only manipulation that took place).

a

b

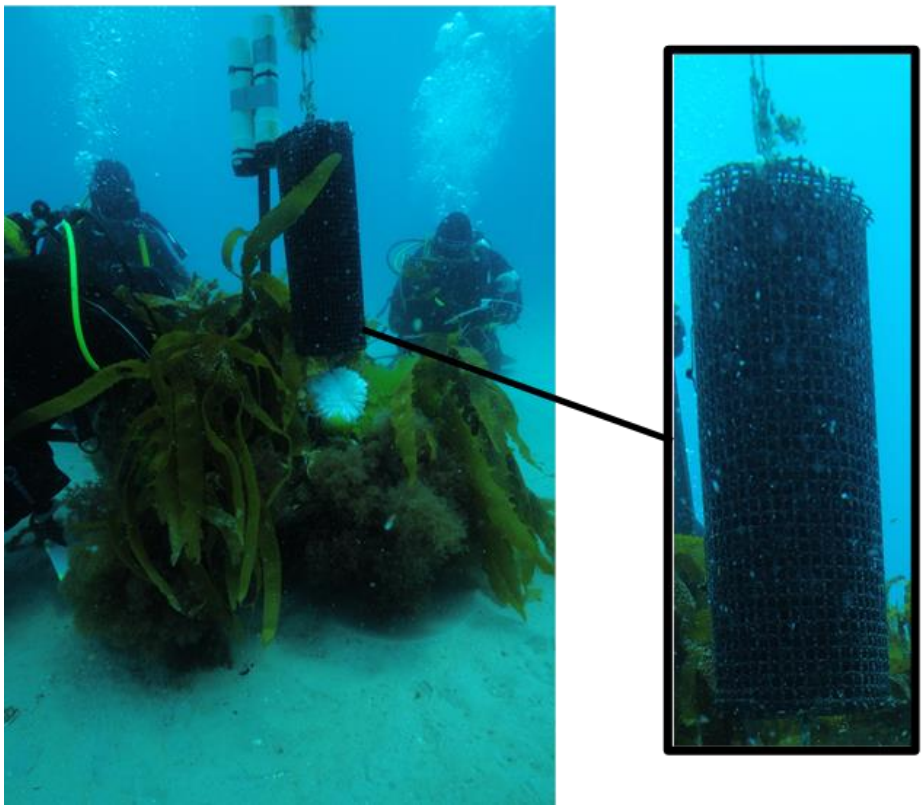

Figure 5.1. Images depicting a) divers working on experimental reefs, and b) A SMURF collector and its position on experimental reefs.

5.3.2 Adult assemblages

Adult fish assemblages were assessed by diver-based visual surveys conducted during three stages of the experiment: early (spring 2015), middle (autumn 2016), and late (spring 2016) (approximately 11, 16 and 23 months after the reefs were deployed respectively). To get a better representation of the fish assemblages at each stage, two separate surveys were conducted (4 – 6 weeks apart) and the results were averaged. Individual surveys were conducted *in situ* with the same diver recording the abundance of all species of fish on and immediately surrounding each reef (within ~ 2 m from the reef edge). This involved the observer first circumnavigating the reef at an elevated height to record vagile species. Cryptic species were then assessed by the diver systematically examining each concrete paver and the associated algae in turn. Finally, the underside of the elevated reef surface was inspected for fishes. The total time needed to survey each reef differed depending on reef area and kelp density, but approximately equal search effort per paver was devoted across reefs supporting a given kelp density.

5.3.3 Recruits

Arrival of recruits was measured using Standard Monitoring Units for the Recruitment of Fish (Ammann 2004) (hereafter abbreviated to *SMURF*), which were deployed in the centre of each reef for a six week period on four consecutive occasions. This collection regime was intended to sample the overall abundance of recruiting fishes drawn to the reefs incorporating outcomes of settlement and post-settlement processes. However, given that SMURFs provided additional structurally complex habitat that was renewed with multiple rounds of deployment, the number of recruits in SMURFs indicates the relative attractiveness of the different reefs for recruiting fishes and not necessarily effective recruitment. Each SMURF (Fig. 5.1b, Appendix C: Fig. C. 1) consisted of a black oyster mesh cylinder (length = 1 m;

diameter = 0.35 m) filled with plastic bio-balls used as pond filtration media (unbranded, 40 mm diameter) that served to provide complex habitat structure (Ammann 2004). SMURFs were collected into 500 µm mesh bags by divers in November and December 2015, and January and March 2016. On the surface, SMURFs were washed over a 500 µm sieve to separate out the fish recruits. Recruits were anesthetised in clove oil and preserved in 70% ethanol before sorting in the laboratory, where they were identified to species under the microscope and the standard length of each individual measured using calipers (Appendix C: Fig. C. 1). Work on fishes complied with ethical guidelines approved by the University of Tasmania's Animal Ethics Committee (Project no. A14511).

5.3.4 Analyses and statistics

The structure of adult fish assemblages based on the density (abundance per unit of reef area) of each species was assessed with multidimensional scaling (MDS), canonical analysis of principal coordinates (CAP), and permutational multivariate analysis of variance (PERMANOVA) based on log-transformed data and Bray-Curtis similarity matrices using PRIMER 6. Due to the high occurrence of zero values on the smaller reefs and inflated densities associated with scaling up from small reefs, we only used data from the two largest patch sizes (4.32 and 7.68 m^2) where densities of individual species could be more reliably estimated. After preliminary investigations revealed that patch size (across the two largest reef sizes) had little effect on the structure of assemblages (Appendix C: Fig. C. 2), we focused on assessing the structure of assemblages in relation to kelp density (0, 4.1, 8.3, 16.6 kelp m^{-2}), and survey time (early, middle and late), where reefs representing the different patch sizes (4.32 and 7.68 m^2) but the same kelp density and survey time were treated as replicates for these analyses.

ANCOVA was used to determine the effects of kelp density (fixed factor) and patch size (covariate) on the abundance, estimated biomass, species richness and Shannon-Wiener (S-W) diversity index for adult assemblages at each of the three stages of the experiment (separately). Biomass was estimated using average biomass values of the different species on nearby reefs at Maria Island (outside marine reserves). This data was collected as part of ongoing monitoring of the Maria Island Marine Reserve (Edgar and Barrett 1999, Soler et al. 2015). ANCOVA was also used to test the effects of kelp density and patch size on the abundance of the two dominant species recruiting to SMURFs, *Parablennius tasmanianus* and *Forsterygion gymnotum*. Analyses were conducted for *P. tasmanianus* and *F. gymnotum* separately and summed together pooling across the four rounds of SMURF deployment, and for both species together in January only (when the peak abundance of recruits was recorded). Model assumptions were checked using diagnostic plots based of model residuals (for normality, linearity and homoscedascity), and the Shapiro-Wilks test for normality. Data transformations were based on the λ coefficient at the maximum log-likelihood using plots produced with the Box-Cox procedure. The covariate (patch size) was $\log_2$ transformed to linearise the data (patch size increased on an approximate a $\log_2$ scale). Homogeneity of slopes was tested by first fitting the saturated ANCOVA model with the interaction term, and if the interaction was non-significant ($P > 0.25$), we proceeded to fit the unsaturated models (i.e. with the interaction term pooled with the within-cells error to provide a better estimate of error). Significant kelp density effects were investigated through pairwise comparisons of covariate adjusted means using the Bonferroni adjustment to significance level to correct for multiple testing (Quinn and Keough 2002) using R (version 3.2.4).

5.4 Results

5.4.1 Adult fish assemblages

MDS and CAP analyses indicated that the structure of fish assemblages varied temporally, with distinct assemblages occurring at the three stages of the experiment (early (spring 2015), middle autumn 2016) and late (spring 2016)) (Fig. 5.2 a, b, Table 5.1). Fewer fish were observed during the early stage, whilst surveys conducted during the middle of the experiment were characterised by an increased abundance of *F. gymnotum*, *A. strigatus, N. balteatus, H. johnstoni* and *C. australis.* At the late stage of the experiment, the characteristic species included *S. attenuatus, D. auranticus* and *P. tasmanianus.* MDS did not indicate any effects of kelp density (Fig. 5.2c), however CAP analysis (which accounted for temporal variability in the assemblages) revealed that fish assemblages associated with reefs without kelp differed from those associated with reefs with kelp (Fig. 5.2d). Reefs without kelp tended to support elevated densities of *P. tasmanianus, F. gymnotum, P. microlepis, A. strigatus* and *S. attenuatues,* whilst reefs with kelp were characterised by an increased dominance of *A. vittiger*, *C. australis*, *S. lineolata* and *P. bachus*. PERMANOVA supported indications from the MDS and CAP analyses and showed a significant effect of time with distinct communities at each of the three stages evident with the pairwise comparisons (Table 5.1). PERMANOVA also supported a significant effect of kelp density, although, the only significant pairwise comparisons occurred between reefs without kelp and those with the medium and low densities of kelp (Table 5.1).

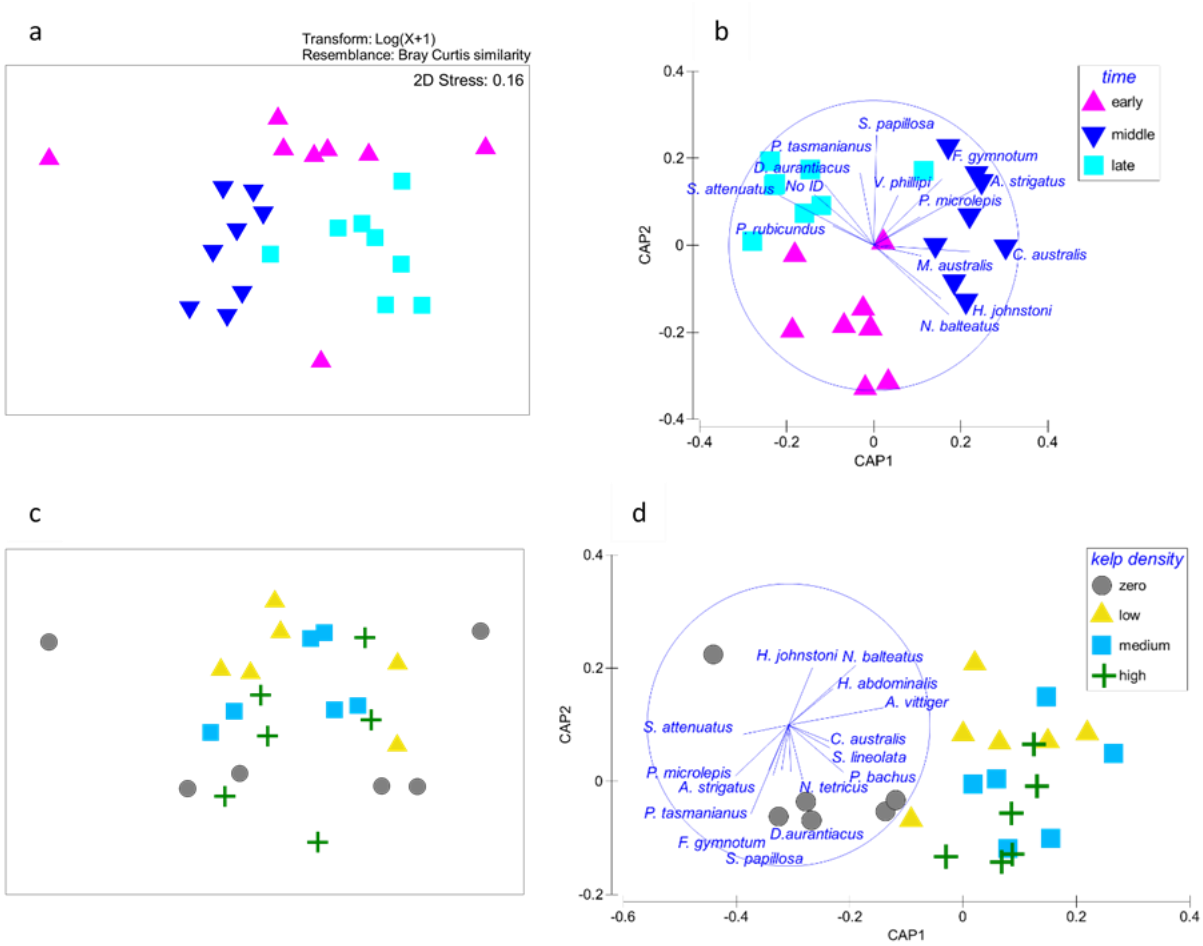

Figure 5.2. MDS (a, c) and CAP (b, d) analyses of the structure of fish assemblages expressed as the density of each species observed on large reefs (≥ 4.32m^2) with different kelp densities at three stages of the experiment (early: spring 2015, middle: autumn 2016, and late: spring 2016), separately labelled to indicate the effects of survey time (a, b) and kelp density (c, d). CAP shown in b) maximizes separation based on time and CAP shown in d) maximizes separation based on kelp density. Vector overlay depicts species with Spearman correlations > 0.3.

source of variation	SS (df)	MS	Pseudo-F	P-value	post-hoc
Kelp density	11783 (3,12)	3927.8	2.30	0.01*	zero ≠ low, medium
Time	22067 (2,12)	11033.0	6.46	0.001*	early ≠ middle late; middle ≠ late
Kelp density x Time	11497 (6,12)	1916.2	1.12	0.32	

Table 5.1. Summary of results of PERMANOVA testing for the effects of kelp density and survey time on the structure of fish assemblages across the two largest patch sizes (4.32 and 7.68 m^2), expressed as the log density of individual species observed in visual surveys across experimental reefs. * indicates significant ($p < 0.05$) effects. Significant post-hoc pairwise comparisons are indicated in the post-hoc column.

Increasing patch size resulted in a significant increase in the abundance, estimated biomass, species richness and S-W diversity index of fishes for all three stages of the experiment (Fig. 5.3, Table 5.2). Kelp density also had significant effects at certain stages, due mainly to differences between reefs without kelp and those supporting the highest density of kelp. Kelp density only had a significant effect on the abundance of fishes during the early stage of the experiment (high > zero) where there were eight times more fish across all reefs with a high density of kelp compared to reefs without kelp (Fig. 5.3a, Table 5.2). Kelp density did not affect estimated biomass early in the experiment, whilst kelp patch size and density interactively affected biomass during the middle stages of the experiment. At the late stage of the experiment biomass was significantly affected by kelp density (high, medium > zero) where reefs with high and medium densities of kelp supported approximately five times greater biomass than the reefs without kelp (Fig 5.3b, Table 5.2). The interactive effect of kelp patch size and density on biomass during the middle of the experiment was removed when reefs with a high density of kelp were omitted. There was no significant effect of kelp density on species richness early in the experiment, although, richness was significantly

greater on reefs supporting a high density of kelp compared to reefs supporting no kelp (by approximately 80 percent) during the middle and later stages of the experiment (Fig. 5.3c, Table 5.2). Patch size and kelp density interactively affected S-W diversity early in the experiment, whilst in the middle stage of the experiment diversity was higher on reefs with the high density of kelp compared to reefs without kelp, and kelp density did not affect diversity at the late stage of the experiment (Fig. 5.3d, Table 5.2). Omitting reefs with zero kelp at the early stage of the experiment removed this interaction between kelp patch size and density on S-W diversity.

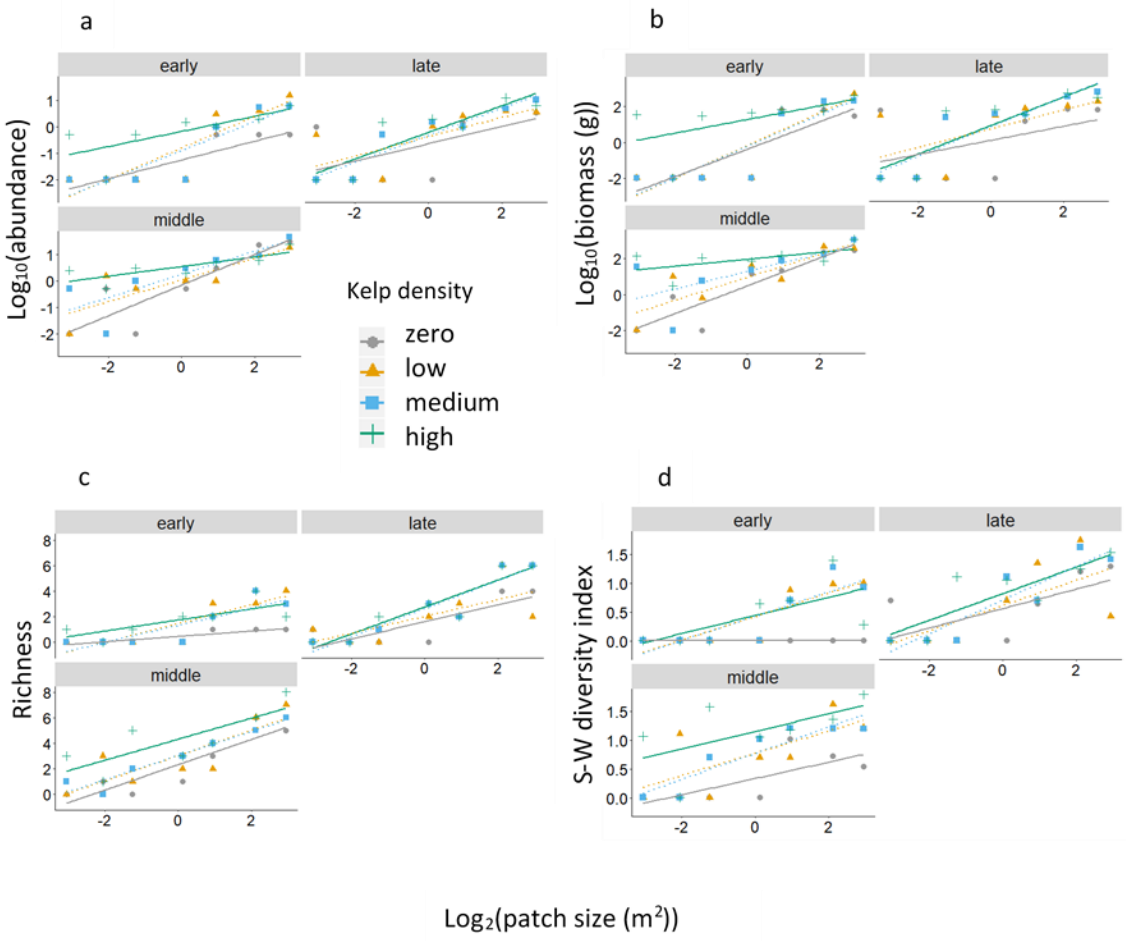

Figure 5.3a) abundance, b) estimated biomass, c) species richness, and d) Shannon-Wiener diversity index of fishes across reefs of different patch size and kelp density at three stages of the experiment (early: spring 2015, middle: autumn 2016, and late: spring 2016). Solid lines highlight comparisons between reefs supporting zero kelp and reefs supporting a high density of kelp.

Model	Factor	SS (df)	F-value	P-value	post-hoc
Adult assemblages: early					
Abundance $Log_{10}(Y)$	Log_2(patch size) Kelp density	23.57 (1,23) 4.31(3,23)	51.22 3.12	< 0.001 * 0.05*	zero < high
Biomass $Log_{10}(Y)$	Log_2(patch size) Kelp density	63.19 (1,23) 12.84 (3,23)	43.52 2.95	< 0.001 * 0.05	
Richness $(Y)^{0.09}$	Log_2(patch size) Kelp density	0.70 (1,23) 0.14 (3,23)	44.65 2.95	< 0.001 * 0.05	
Diversity $(Y)^{-0.44}$	Log_2(patch size) * Kelp density	40.77 (3,20)	5.05	0.01 *	
Diversity (omitting reefs with zero kelp) $(Y)^{-0.13}$	Log_2(patch size) Kelp density	2.44 (1,17) 0.03 (2,17)	49.61 0.35	0.01 * 0.71	
Adult assemblages: middle					
Abundance $(Y)^{0.19}$	Log_2(patch size) Kelp density	4.17 (1,23) 0.22 (3,23)	66.72 1.15	< 0.001 * 0.35	
Biomass $(Y)^{0.13}$	Log_2(patch size) * Kelp density	6.76 (3,19)	3.29	0.04*	
Biomass (omitting reefs with a high density of kelp) $(Y)^{0.15}$	Log_2(patch size) Kelp density	8.96 (1,16) 0.14 (2,16)	103.81 0.82	< 0.001 * 0.45	
Richness $(Y)^{0.55}$	Log_2(patch size) Kelp density	21.14 (1,23) 2.66 (3,23)	82.21 3.45	< 0.001 * 0.03 *	zero < high
Diversity $(Y)^{0.46}$	Log_2(patch size) Kelp density	2.34 (1,23) 0.35 (3,23)	25.53 3.88	< 0.001 * 0.02 *	zero < high
Adult assemblages: late					
Abundance $(Y)^{0.25}$	Log_2(patch size) Kelp density	5.18 (1,22) 0.43 (3,22)	79.76 2.22	< 0.001 * 0.11	
Biomass $(Y)^{0.22}$	Log_2(patch size) Kelp density	27.67 (1,22) 5.25 (3,22)	65.48 4.14	< 0.001 * 0.02 *	zero < medium, high
Richness $(Y)^{0.46}$	Log_2(patch size) Kelp density	11.49 (1,22) 1.86 (3,22)	70.63 3.82	< 0.001 * 0.03 *	zero < high
Diversity $(Y)^{0.19}$	Log_2(patch size) Kelp density	1.66 (1,22) 0.13 (3,22)	61.39 1.63	< 0.001 * 0.21	
Recruits					
Total $(Y)^{0.44}$	Log_2(patch size) Kelp density	7.49 (1,22) 4.73 (3,22)	15.09 3.18	< 0.001 * 0.04 *	zero > low
January $(Y)^{0.29}$	Log_2(patch size) Kelp density	1.90 (1, 23) 1.33 (3, 23)	15.22 3.56	< 0.001 * 0.030 *	high > low
P. tasmanianus $(Y)^{0.42}$	Log_2(patch size) Kelp density	5.98 (1, 23) 6.02 (3, 23)	20.94 7.02	< 0.001 * 0.002 *	zero, high > low
F. gymnotum $(Y)^{0.39}$	log_2(patch size) kelp density	7.09 (1, 23) 2.54 (3, 23)	20.37 2.43	< 0.001 * 0.094	

Table 5.2. Summary of results of ANCOVA testing for the effects of kelp patch size and density on fishes at three stages of the experiment (early: spring 2015, middle: autumn 2016, and late: spring 2016) and on the abundance of post-larval recruits in SMURF collectors between November 2015 and March 2016. Response variable transformations are shown in terms of the untransformed variable Y. The covariate (patch size) was $\log_2$ transformed. Significant ($p < 0.05$) effects are indicated by *. Significant post-hoc pairwise comparisons are indicated in the post-hoc column.

5.4.2 Recruits

252 post-larval recruits were collected across the entire recruitment period (November 2015 to March 2016) and 89% of those were either *P. tasmanianus* (47%) or *F. gymnotum* (42%). The total abundance of recruits in SMURFs declined significantly with kelp patch size, and reefs with zero kelp had more than two times higher recruit numbers than reefs with kelp at low densities (Fig. 5.4; Table 5.2). A similar pattern was evident for recruitment in January alone (the month with the highest abundance of recruits) aggregating across species, and for *P. tasmanianus* recruits across the four SMURF collection rounds. However, total abundance of *P. tasmanianus* recruits was higher on reefs supporting zero and high densities of kelp compared to reefs with the low density of kelp, and recruitment in January was only elevated on reefs with a high density of kelp compared to reefs supporting low densities of kelp. *F. gymnotum* showed a similar recruitment pattern to *P. tasmanianus*, but the effect of kelp density was not significant.

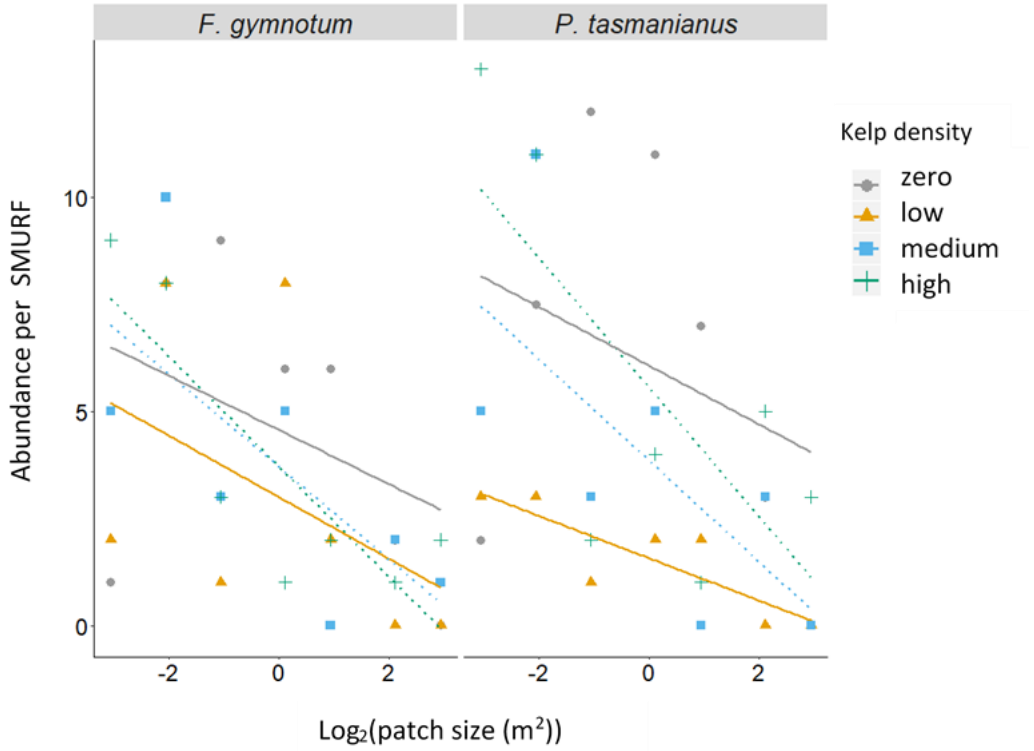

Figure 5.4. Abundance of a) *Parablennius tasmanianus* and b) *Forsterygion gymnotum* recruits collected in SMURF fish collectors across reefs of different size and kelp density pooled across four sampling times between November 2016 and March 2016.

5.5 Discussion

Despite temporal variability in the structure of assemblages, fish abundance, estimated biomass, species richness and S-W diversity index increased with patch size at all three times and tended to be higher on reefs supporting dense kelp stands compared to those without kelp. Unexpectantly, however, the abundance of recruits in SMURFs declined with increasing patch size and there tended to be more recruits in SMURFs on reefs without kelp and kelp at a high density compared to the reefs with a low density of kelp. Overall, our findings demonstrate that *E. radiata*, especially at high densities, enhances the capacity of habitat patches to attract biodiverse fish assemblages. *E. radiata* is also likely to have a

complex role mediating the recruitment and/or behaviour cryptobenthic species which do not appear to directly depend on kelp for habitat.

5.5.1 Influence of patch size on adult assemblages

Not surprisingly, increasing habitat amount (i.e. patch size) positively influenced fish assemblages (abundance and biodiversity), and this corresponded with increases in total epifaunal secondary productivity (but not on a per unit area basis) and macroalgal refuge provided by *E. radiata* and foliose algal species (Shelamoff et al. 2019, Shelamoff et al. 2020). The log density of fish abundance and the log density of species richness were highly variable across patches of similar size, but both responses were positively affected by increasing patch size (Appendix C: Fig. C. 3). This suggests that larger patches provided greater benefit to fish assemblages than smaller patches of equivalent area spanning the range of patches sizes used in this study (Deza and Anderson 2010, Watling et al. 2020). This finding contrasts with studies in terrestrial systems that indicate that biodiversity is primarily driven by habitat availability rather than patch size *per se* (Watling et al. 2020) and is also contrary to the asymptotic relationship between fish density and *M. pyrifera* patch size that occurred for patches that were an order of magnitude larger than the patches we examined (Deza and Anderson 2010). This discrepancy may also be influenced by very low levels of connectivity between the reefs used in this study (see 5.5.5 below). Furthermore, comparisons with *M. pyrifera* may be of limited value given the vast difference in the size and morphology of this species compared to *E. radiata*. The beneficial effect of kelp presence and patch size that we observed suggests that fish assemblages are likely to be affected by both the amount of kelp habitat and patch configuration (albeit for small and relatively isolated patches). It should be noted however, that our findings should not extrapolated to larger patches (10s to > 100s m^2) where populations/communities are likely to be driven by different processes

(Witman et al. 2015). Similarly, despite differences in the attractiveness of the different reefs, the population dynamics of vagile species are unlikely to affected by the different reefs used in this study due to their capacity to move freely across the landscape. Instead, these species are likely to respond to patches occurring at much larger spatial scales (kms) (Lamy et al. 2018).

5.5.2 Influence of patch size on recruits

The decrease in the abundance of recruits in SMURFS with patch size was contrary to expectation. However, given that only a single individual of either species (*P. tasmanianus* or *F. gymnotum*) was recorded on reefs < 1m^2 in visual surveys after the recruitment period, whilst six reefs ≥ 1.92 m^2 supported these species, we are not convinced that small patches provided increased support for these species. We suspect that on small reefs, larval and post-larval fishes had a limited capacity to spread out across the habitat and were more concentrated around the SMURF. Thus, rather than providing a representative sample of the total abundance of recruits per reef, SMURFs may have sampled the density of recruits around the reef. Scaling the number of recruits in SMURFs by reef area indicates a potential increase in recruit abundance with patch size. It is possible that the large size of the SMURFs compared to small reefs (Fig. C. 1) could have led to disproportionate sampling of recruits across the reef sizes and the SMURFs. However, it should be noted that the size of the SMURFs was equal across the reefs and these devices function to attract fish from the surrounding water column (an area much larger than the SMURF) not just the reef itself. Several other studies are consistent with our finding that smaller habitat patches attract elevated densities (but potentially a lower total abundance) of recruits compared to larger patches (Schroeder 1987, Morton and Shima 2013). In contrast, Deza and Anderson (2010) found no significant effect of habitat area on recruit density of kelp dependent fishes within a

Macrocystis pyrifera forest over a similar range of patch sizes to that used in this study. High densities of recruits on small reefs could indicate that these habitats were of higher quality for recruiting cryptobenthic fishes (on a per unit area basis) which could be influenced by the reduced number of adult fishes (potential predation effects) and the higher concentrations of epifaunal secondary productivity (food resources) on small reefs dominated by filamentous algal turfs (Shelamoff et al. 2020). However, larval settlement is unlikely to increases linearly with patch, while it is likely to flatten out (Keough 1984, Morton and Shima 2013). This flattening out could also explain the reduced densities of recruits on larger reefs irrespective of habitat quality. Given the relatively high abundances of *P. tasmanianus* and *F. gymnotum* recruits on reefs without kelp, reductions in kelp patch size (corresponding with an increase in deforested rocky reef) could positively influence recruitment of these species. Higher densities of recruits on smaller reefs also suggests a positive influence of kelp habitat fragmentation on these species.

It is also possible that the abundance of recruits in SMURFs was not completely representative of the number of recruits arriving to the reefs. The high abundance of recruits in some SMURFs (especially those on small reefs) in combination with the relatively low frequency of sampling of the SMURFs (at six-week intervals) may have led to density-dependant mortality and possible underestimation of the arrival of recruits to these reefs. Biological interactions and/or behavioural factors may also have had a pronounced effect on recruits if recruits had a reasonably high affinity to the reef substratum relative to the SMURF. Under this circumstance, habitation of SMURFs may have been influenced by interspecific and intraspecific competition for space on the substratum i.e. under high competition more recruits may be driven to the SMURF. Alternatively, SMURF habitation could have been influenced by the threat of predation In that case, when the threat of

predation is low, recruits may exhibit more foraging/exploratory behaviour above the reef surface (Steel et al. 2019) which could increase numbers associated with the SMURF. Although it is not certain that recruitment to SMURFs was indicative of recruitment to the reefs, it seems unlikely that we would have recorded such high numbers of recruits if SMURFs did not provide an attractive habitat. Furthermore, similarly designed SMURFs have effectively been used to assess the recruitment of similar species to *P. tasmanianus* and *F. gymnotum* in studies elsewhere (Ammann 2004, Shima and Swearer 2009, Morton and Shima 2013). Nevertheless, *P. tasmaniaus* and *F. gymnotum* recruits appear to respond to kelp patch size and density in complex ways.

5.5.3 Influence of kelp density on adult assemblages

The observed positive effect of *E. radiata* at high densities on the abundance and species richness of fishes is consistent with findings within forests of *Sargassum filipendula* and *Lessonia trabeculata* (Levin and Hay 1996, Perez-Matus et al. 2007). High densities of kelp are likely to provide a larger amount of three-dimensional habitat and possibly stronger visual, auditory, and olfactory cues, attracting greater numbers of fishes from surrounding areas (Levin and Hay 1996, Rossi et al. 2017). Although few fishes consume *E. radiata* directly in southern Australia, epifauna associated with fronds may provide an additional food resource supplementing already high levels of epifaunal secondary productivity associated with understory algae on the reefs with high densities of kelp (Shelamoff et al. 2020). Dense kelp in combination with foliose understory algae may also provide improved refuge from larger predatory fishes, although algal refuge tends to correlate better with the abundance of smaller juveniles fishes than larger individuals (Holbrook and Schmitt 1984, Carr 1989). Reduced species richness on reefs without *E. radiata* appeared to be influenced by the absence of kelp associated species (e.g. *A. vittiger, C. australis* etc.), whilst the species

that colonised these reefs also occurred on reefs with kelp (generally in lower numbers). Reefs with dense kelp probably provided greater structural complexity and variety of microhabitats, as well as increased food and refuge, which can positively influence biodiversity (Teagle et al. 2017, Layton et al. 2019b, Shelamoff et al. 2019, Shelamoff et al. 2020).

5.5.4 Influence of kelp density on recruits

The non-linear effect of kelp density on recruitment to SMURFs (reefs with zero kelp and kelp at high density supported greater recruitment than reefs with kelp at low density) contrasts with previous studies indicating either positive (Carr 1989, Siddon et al. 2008, White and Caselle 2008) or negative (Levin 1993, Pérez-Matus et al. 2016) effects of kelp density on recruitment. However, our finding was consistent with Morton and Shima (2013) and Levin (1994a) who observed an adverse effect of dispersed habitat structure (versus clumped) on recruitment of cryptic fishes. We found only one other study that reported a non-linear effect of any type of habitat structure on fish recruitment (Andrews and Anderson 2004), where recruitment was either highest or lowest with a medium cover of rocky substrata (compared to low and high cover) dependent on the fish species. We suspect that these kinds of non-linear responses to habitat complexity may be more prevalent than is reflected in the literature, especially in situations where increasing complexity has both positive (e.g. reduced predation risk) and negative (e.g. reduced food resources) effects on associated species. Indeed, interactive effects of multiple factors including food availability, refuge from predators, as well as the abundance of predators and conspecifics, have been shown to influence recruitment (Schmitt and Holbrook 1985, Shulman 1985, Hunt et al. 2011). Similarly, there is unlikely to be a simple explanation pertaining to behaviour that explains the aversion of recruits to SMURFs on reefs supporting low densities of kelp.

5.5.5 Implications

Our results shed light on some of the potential consequences of an increase in kelp forest patchiness. Principally, smaller patches attract fewer fishes and fewer species. The impact of reductions in kelp density are less clear, although dense kelp stands are likely to attract the highest number of species. Some populations of cryptobenthic species are probably relatively robust to (and even benefit from) kelp loss and declines in patch size, but they may be negatively impacted by declines in kelp density. We need to better understand the behaviour of larval and post-larval fishes to fully understand how populations are likely to respond to kelp loss. Extension of our findings to fully natural ecosystems, requires some caution. In particular, the reefs themselves may not have been fully representative of natural rocky reef, levels of connectivity between artificial reefs and connectivity to surrounding natural reef were likely to have been very low (due to the distance between reefs and the poor-quality of the surrounding sandy habitat), and the assemblages colonising the reefs probably contained only a small subset of species that typically colonise rocky reefs in the area, thus the reefs did not capture the full range of species interactions which can influence fish assemblages. Nonetheless, it is clear that kelp generally benefits fish assemblages at the microhabitat scale, although with a multitude of other factors that can additionally influence assemblages.

Our findings also have implications for kelp forest restoration, and the need to better understand design characteristics that enhance the establishment of fish assemblages around artificial reefs (Baine 2001). Similar to studies on *M. pyrifera*, we show that adding *E. radiata* to coastal areas attracts fishes and changes the composition of species (Reed et al. 2006, Villegas et al. 2019). Adding dense kelp and increasing the size of patches/reefs (probably far beyond 7.68 m^2) is likely to further increase the biomass and species richness of

fishes, although the spatial configuration of the reefs will also be important (Jordan et al. 2005). It might also be possible to boost the productivity of some cryptobenthic species through deploying multiple small (< 1 m^2) artificial reefs without kelp close to natural reef. However, we suspect that small isolated reefs could act as fish recruitment 'sinks' or ecological traps, which attract recruits but do not provide sufficient resources overall to support their transition to adulthood (Rishworth et al. 2017). The proximity of the reefs to other habitat as well as the post-recruitment dispersal capability of target species are likely to influence the capacity of artificial reefs to support nearby populations.

5.5.6 Conclusions

Our results demonstrate that structural complexity provided by dense canopies of kelp attracts fishes and promotes biodiversity, whilst some fish populations may show a different and more complex response to canopy structure. Establishing kelp on natural and artificial structures, even in small amounts, is likely to benefit fish assemblages and help support the ecosystem. This presents opportunities for eco-engineering and enhancing the coastal environment, albeit at relatively small scales.

Acknowledgements

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Chapter 6. General discussion

6.1 Synthesis of results

This research aimed to experimentally determine the role of *Ecklonia radiata* patch size and density in influencing: the composition of understory algae and sessile invertebrates (chapter 2), *Ostrea angasi* recruitment (chapter 3), secondary productivity and biodiversity of epifaunal invertebrates (chapter 4), and the composition of fish assemblages including the abundance of recruiting cryptobenthic species (chapter 5). This research used an array of artificial reefs where *E. radiata* patch size and density could be accurately manipulated and where the effects of *E. radiata* structure (i.e. patch size and density) on the abiotic environment (sub-canopy: light, water flow, sediment deposition and sediment accumulation) had previously been quantified (Layton et al. 2019b). Data from Layton et al. (2019b) in combination with results from chapters 2 – 5 permitted exploration of the role of abiotic and biotic ecosystem engineering by *E. radiata* in driving community dynamics. By highlighting how the assembly of diverse organisms, spanning multiple trophic levels and functional groups, was affected by variability in kelp structure of this dominant kelp species, this thesis makes a substantive contribution to our understanding of kelp forest patch dynamics.

Kelp structure was instrumental in shaping benthic communities of sessile organisms (chapters 2, 3). Small patch size and absence of kelp led to a high dominance of filamentous algal turfs, whilst larger patches with low and medium densities of kelp were dominated by foliose algae and had a high abundance of sessile invertebrates (mainly the native oyster *Ostrea angasi*). Kelp appeared to influence understory sessile assemblages predominantly through their capacity to reduce the availability of sub-canopy light (i.e. canopy shading).

The complete (or near complete) absence of a canopy which resulted in high transmission of light to the benthos, allowed for fast growing algal turfs to flourish. In contrast, a fuller canopy appeared to reduce benthic light levels sufficiently to suppress the growth of turf algae and allow for foliose species and sessile invertebrates to expand across the benthos. Potentially, very low levels of sub-canopy light on larger reefs with the highest density of kelp additionally reduced the growth and abundance of foliose algae on these reefs. The strong negative correlation between cover of turf algae (which established rapidly on the artificial reefs) and cover of foliose algae and *O. angasi* (which were slower to establish), supports the notion that turfs had a strong influence in shaping the composition of other sessile species through their competitive dominance under a high light environment. The capacity of canopy-forming kelp to suppress turf algae via the reduction of benthic light levels has been described in other studies (Airoldi 1998, Irving and Connell 2002, Connell 2005, Russell 2007, Reeves et al. 2018) and the tendency for turf algae to suppress other sessile species has also been demonstrated (Kennelly 1987a, Gorgula and Connell 2004, Isæus et al. 2004, Wernberg et al. 2016, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). The results described in chapter 2 support the notion that both abiotic (i.e. light transmission) and biotic (i.e. cover of turf algae) ecosystem engineering by kelp are instrumental in shaping the composition of understory sessile species.

Kelp structure also strongly influenced the productivity of mobile epifauna associated with the understory (chapter 4). Secondary production in this form provides a critical trophic link in coastal food webs and therefore could indicate food resource availability for higher order consumers such as larger invertebrates and fishes (Edgar and Shaw 1995b, Taylor 1998). Secondary productivity of these epifaunal meso-invertebrates amongst sub-canopy algae declined with kelp patch size and had a non-linear response to kelp density, in that

productivity was highest when kelp was either absent or at the highest density compared to when kelp was at intermediate densities. Epifaunal productivity appeared to be influenced by the composition of understory algae and abiotic ecosystem engineering. There was an elevated abundance of the foliose alga *Ulva.* sp. on reefs supporting low kelp densities and the abundance of *Ulva* sp. was strongly (negatively) correlated with secondary productivity. The influence of *Ulva* sp. on secondary productivity likely obscured weaker but still contributory, abiotic influences including water flow and light. Epifaunal productivity associated with standardised artificial habitats which excluded the influence of understory algae, indicated that light was also a major driver of epifaunal productivity. These results are consistent with other research findings which show that abiotic factors, especially light (Edgar and Aoki 1993, Eilertsen et al. 2011), in addition to biotic factors i.e. algal structure (Hacker and Steneck 1990, Parker et al. 2001, Chemello and Milazzo 2002), influence secondary productivity of epifauna by modifying the availability of food (i.e. microphytobenthic algae) and refuge. This chapter highlights links between kelp structure, sessile assemblages (i.e. understory algae) and mobile assemblages (i.e. epifauna), which could have implications for coastal food webs more broadly.

Increased kelp patch size and density positively influenced the abundance and species richness of the fishes associated with the reefs, whilst there was a negative effect of kelp patch size and a non-linear effect of kelp density on recruiting cryptobenthic species (i.e. the abundance of recruits in SMURF collectors was lower on reefs with low densities of kelp compared to reefs without kelp or those with the highest kelp density) (chapter 5). Fish assemblages may have responded positively to kelp associated cues (visual, olfactory, acoustic etc.), increased structural complexity, and/or increased availability of food and refuge. Recruitment and/or behaviour of cryptobenthic species showed a complex response to

kelp structure, which may have been influenced by multiple factors (i.e. ecosystem engineering effects) including possible negative effects of planktivorous and invertivorous fish (predation effects) and possible positive effects of secondary productivity (food resource availability). However, further investigation is needed to rule out experimental artefacts influencing the arrival of recruits to SMURFs. Although not commonly reported, non-linear response to habitat structural complexity (e.g. kelp density) may occur when increasing complexity simultaneously affects both positive (e.g. provision of food) and negative (e.g. predation pressure) influences of habitat quality.

Overall, this thesis demonstrates that kelp structure is a major driver of the composition of benthic communities spanning multiple trophic levels by influencing the local environment and the abundance of other influential species. Kelp patch dynamics therefore entail complex and profound community variability. It then follows that different manifestations of kelp loss (e.g. fragmentation, canopy thinning etc.) or habitat creation are likely to lead to different outcomes for the diversity, composition and productivity of the associated communities.

6.2 Study limitations

Use of artificial reefs permitted a high level of control around providing consistent kelp patch size and density treatments which could act relatively independent of other factors that were not the focus of this research but can nonetheless influence communities (e.g. topography, the surrounding habitat matrix, influential species such as sea urchin grazers). This experimental control would not have been possible working within highly variable natural kelp forest systems. Although this approach helped ensure that the assemblages associated with the reefs responded to kelp structure (and associated effects of ecosystem engineering) and not other

factors, there is the potential limitation that the observed responses may not truly reflect community dynamics within fully natural ecosystems.

There are a number of issues relating to the scale of the experiment that need to be considered. The fact that the experimental reefs were separated from one another by 25m and over 1.5km from the nearest natural rocky reefs generated high levels of isolation between patches (i.e. reefs). This level of isolation is beyond the scale that is likely to be relevant to natural kelp forest ecosystems subject to fragmentation. Furthermore, the sandy substratum surrounding the reefs probably provided lower levels of connectivity between patches than would occur on continuous rocky reef with patchy kelp habitat. Although the size of patches examined in this study (0.12 – 7.68m^2) are useful for understanding community assembly at the microhabitat level and for elucidating threshold habitat requirements and effects of severe habitat fragmentation, the observed responses should not be extrapolated to larger scales (10s to >100s m^2) where communities are likely to be driven by different processes. Similarly, the population dynamics of vagile organisms such as many fishes are unlikely to be affected by the range of patch sizes in these experiments (despite differences in the attractiveness of the different reefs) due to their capacity to move freely across the landscape. Instead, these species are likely to respond to patches occurring at much larger spatial scales (kms) (Lamy et al. 2018). It is also possible that the use of SMURFs, which were large in comparison to the size of small reefs, led to disproportionate sampling of recruiting fishes across the reefs. Furthermore, it was not feasible to repeat this experiment across time or multiple locations (due to time and financial constraints), which would provide greater support for the generality of the findings.

The composition of the species that colonized the reefs are also likely to differ from those associated with natural systems. Consequently, some important and influential species and species interactions were either absent or would have occurred at different levels across the array of artificial reefs compared to levels of natural reefs. In particular, the fact that the reefs were located away natural rocky reefs and were elevated off the substratum prevented influential sea urchin grazers from colonising the reefs. Urchins can have a large effect on community dynamics through the destructive grazing of macroalgae (Ling 2008); however, the absence of urchins was necessary to maintain consistent kelp cover. It should be noted though, that intact kelp beds are likely to reduce the capacity of urchins to degrade the ecosystem (Kriegisch et al. 2019), which could indicate that smaller and less dense kelp patches have lower resistance to these grazers. The experimental reefs were also only deployed for a period of two years, which may not have been a sufficient period for them to develop mature reef communities. Finally, the concrete pavers used to construct the reefs may have impacted community establishment by providing different levels of refuge and other resources compared to natural rocky reef habitat.

However, despite these caveats, the results of this investigation are likely to have broad relevance to other systems. The effects of kelp structure on the abiotic environment quantified across the artificial reefs by Layton et al. (2019b) is largely consistent with how kelp modifies the subcanopy within natural kelp forest systems (Eckman et al. 1989, Kennelly 1989, Irving and Connell 2002, Connell 2005, Wernberg et al. 2005). Moreover, many of the observed effects of kelp structure and ecosystem engineering on turf algae, foliose algae, sessile invertebrates, mobile epifaunal invertebrates, and fish communities, are also consistent with observations from natural rocky reefs (Kennelly 1989, Edgar and Aoki 1993, Levin and Hay 1996, Roberts and Poore 2006, Deza and Anderson 2010, Flukes et al.

2014). By manipulating only the patch size and density of *E. radiata*, this research demonstrates the fundamental importance of kelp structure in driving community dynamics. However, within fully natural systems a range of additional factors (e.g. connectivity, influential species, topography etc.) are also likely to influence communities. By examining the responses of a broad suite of organisms and by focusing on broad functional groups and community metrics such as species richness and diversity as opposed to individual species, these research findings provide general insights into kelp patch dynamics.

6.3 Kelp loss scenarios

Although the creation of novel habitat representing a gradation in kelp cover is not necessarily equivalent to having kelp habitat that has experienced incremental levels of decline, these research findings can nonetheless be extended to indicate possible effects of various kelp loss scenarios. By comparing the communities associated with large kelp patches to those associated with small kelp patches (loss of patch size) and by comparing the communities on reefs with high densities of kelp to those on reefs with low densities of kelp (loss or kelp density) or no kelp (complete loss of kelp), it is possible to make predictions about how communities respond to different types of kelp loss (although consideration should be given to the limitations described above). This application is not inappropriate given that kelp structure appears to affect the abiotic environment and the associated communities in a relatively consistent manner, regardless of whether kelp is added to, or removed from the system (see section 6.2 above). The experimental chapters of thesis indicate that vastly different communities are likely to result from complete loss of kelp versus a thinning density (Fig. 6.1). The degree of a reduction in patch size is also likely to be important, with very different communities likely to be associated with patches > $2m^2$ compared to patches < $1m^2$

(Fig. 6.2). It is therefore important to consider the type and degree of habitat loss that is occurring at a particular location to anticipate the consequences for associated communities.

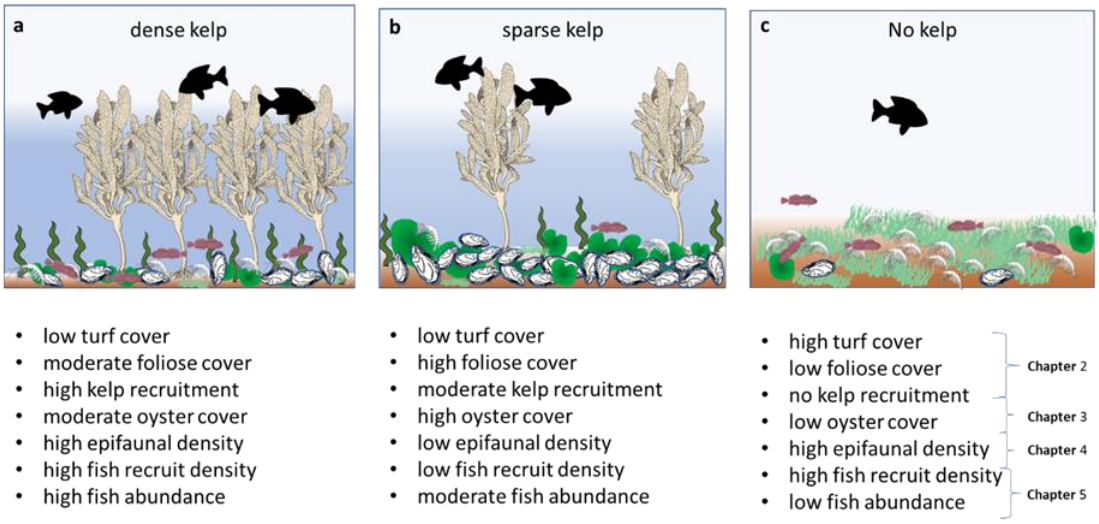

Figure 6.1. Diagram summarising observed effects of a) dense kelp, b) sparse kelp and c) complete absence of kelp on associated communities based on experiments described in chapters 2 - 5. See Fig. 6.1 for symbol ID.

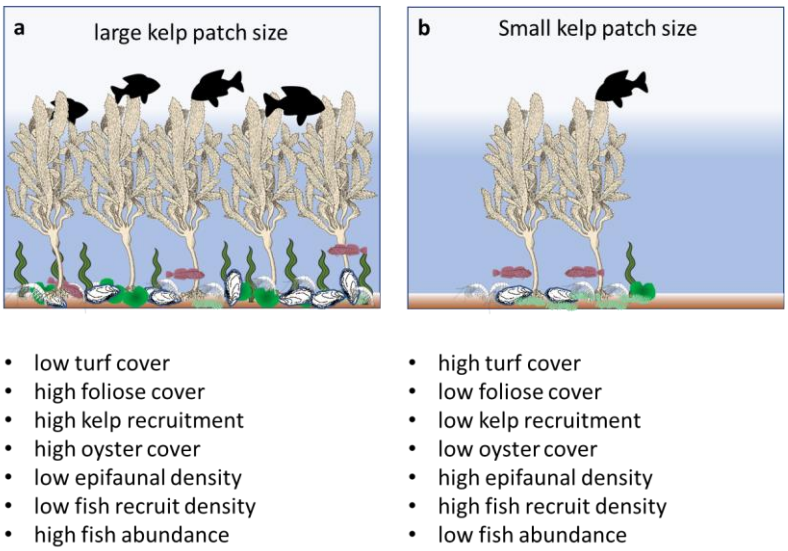

Figure 6.2. Diagram summarising observed effects of a) large and b) small kelp patch size on associated communities based on experiments described in chapters 2 - 5. See Fig. 1.2 for symbol ID.

Complete kelp loss and small patch size are likely to lead to the dominance of filamentous algal-turfs which tend to trap sediments and may form a chemically distinct boundary layer

(Connell et al. 2014, Short et al. 2015, Filbee-Dexter and Wernberg 2018, Reeves et al. 2018, Layton et al. 2019a). These assemblages can stifle the growth and development of other algae including canopy-forming kelp resulting in an alternative stable state (Kennelly 1987a, O'Brien and Scheibling 2018). Turf-dominated rocky reefs are likely to support elevated levels of epifaunal productivity (i.e. secondary productivity), especially in relation to the biomass of the algal habitat (Miller et al. 2009, Lavender et al. 2017). Hence, turfs may provide abundant food resources for higher trophic order consumers such as fishes and macroinvertebrates; however, turfs lack the structural complexity required to provide suitable refuge for larger mobile species (Filbee-Dexter and Wernberg 2018). Some species (e.g. mesograzers such as amphipods) may be able to effectively exploit turf-dominated habitat, whilst many others may avoid these areas. Overall, turf-dominated reefs are likely to be detrimental to biodiversity as indicated by their homogenous epifaunal assemblages (chapter 4) and the reduced richness of fish species (chapter 5) that were observed on reefs without kelp.

An alternative benthic assemblage may also result from a persistent reduction in kelp density but maintenance of patch sizes > $2m^2$. Larger artificial reefs with kelp at low densities supported understories dominated by foliose algae (especially *Ulva* sp.) and accompanied by a high abundance of native oysters (*Ostrea angasi*) (chapters 2 - 3). Similar foliose algae dominated ecosystem states have been recognised in other studies (Miller et al. 2009, Flukes et al. 2014); however, it has not been adequately established whether these states represent a transient or stable phase. Understories dominated by *Ulva* sp. supported reduced secondary productivity (chapter 4), which could indicate a widespread adverse consequence of declining kelp density. Although areas with low densities of kelp and an *Ulva*-dominated understory are likely to support less productive food webs, these areas could provide much higher levels

of structural complexity and refuge than areas dominated by turfs, and this could benefit larger macroinvertebrates and fishes (Wilson et al. 1990). Although, the most diverse and species rich fish assemblages were associated with dense kelp cover and moderate cover of foliose algae (chapter 5). The potential for rocky-reef habitat to support fishes and macroinvertebrate assemblages will likely depend on a range of factors including the availability of food and refuge.

6.4 Ecosystem stability

The species associated with kelp habitat have a major bearing on the resistance of kelp forest ecosystems to degrade and transition to undesirable ecosystem states. Two degraded ecosystem states are well recognised as alternative stable states for kelp forest ecosystems. A *barren ecosystem stat*e, which is created through high levels of grazing by sea urchins, is characterised by the absence of macroalgae and low levels of productivity and biodiversity (Steneck et al. 2002, Ling 2008, Filbee-Dexter and Scheibling 2014, Steneck and Johnson 2014). The second state is a *turf-dominated state,* which occurs when turf algae dominates reef substratum and suppresses that establishment of other macroalgae (see above) (Kennelly 1987a, Gorgula and Connell 2004, Isæus et al. 2004, Connell Sean and Russell Bayden 2010, Wernberg et al. 2016, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). Preventing the occurrence of these undesired states is critical in maintaining healthy and productive kelp forest ecosystems.

In southern Australia, the range-expanding long-spined sea urchin (*Centrostephanus rodgersii)* is the major barren-forming urchin species. However, as none of our reefs were subject to grazing by these urchins, the communities associated with urchin barrens were not

represented on the experimental reefs. Importantly though, relatively high numbers of southern rock lobsters (*Jasus edwardsii*) recruited to the reefs. Large lobsters are the only known native predator of these urchins capable of having a meaningful impact on their populations in Tasmania; however, in many areas lobster numbers have decreased substantially due to overfishing (Ling et al. 2009a). The recruitment of lobsters and their development into large individuals is therefore likely to support the resistance of kelp forest ecosystems to over-grazing by sea urchins. Data collected across the experimental reefs, but not included as part of this thesis, showed that lobster recruitment was highest on larger kelp patches supporting medium and low densities of kelp (Fig. 6.3). Lobster populations may therefore be robust to some level of decline in kelp density but are likely to be susceptible to complete loss of kelp or a reduction in patch size.

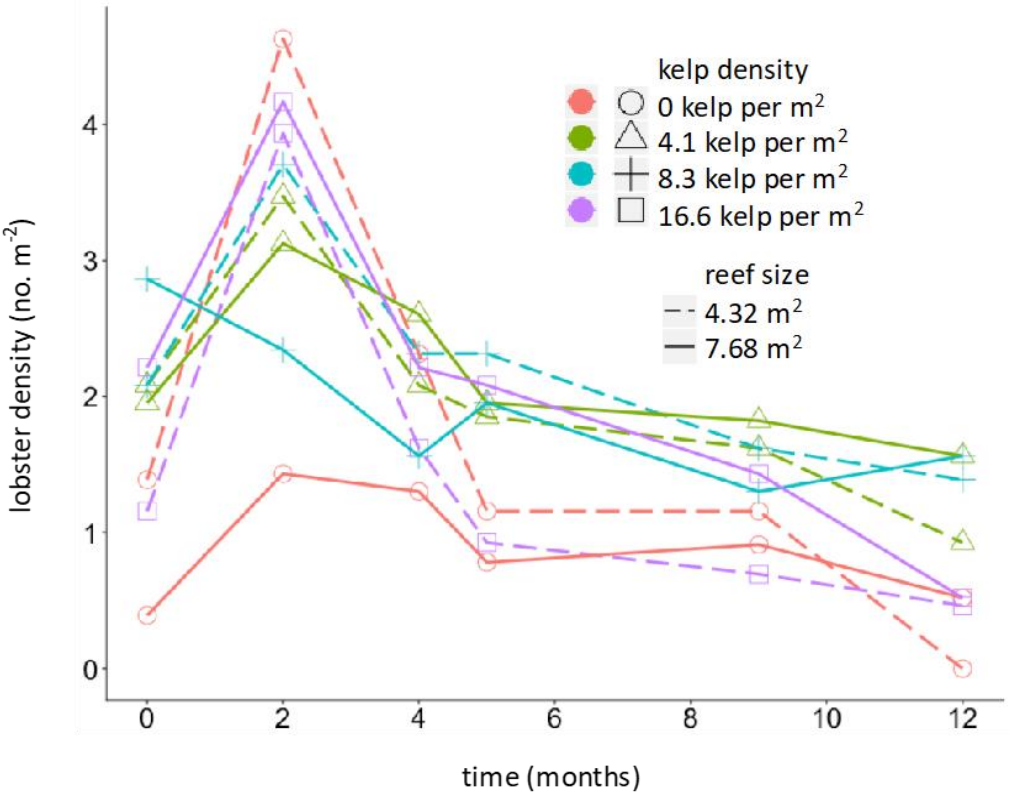

Figure 6.3. *Jasus edwardsii* density (no. m^{-2}) on 2 largest experimental reef sizes (4.32 m^2 and 7.68 m^2) supporting four 4 densities of kelp (0 – 16.6 kelp m^{-2}) through time. Lobster densities were determined by diver-based visual surveys conducted during different months

between November 2015 (time = 0) and November 2016 (time = 12) (11 – 23 months after the initial deployment of the reefs).

Kelp are themselves important in resisting phase shift to a state dominated by algal turfs. Kelp resist turf establishment through canopy-shading, sweeping away sediment that is deposited on the reef surface, and by scouring and damaging understory filamentous algae with their laminae in surge (Connell 2005, Russell 2007, Filbee-Dexter and Wernberg 2018, O'Brien and Scheibling 2018, Reeves et al. 2018). Kelp loss is therefore likely to lower the resistance of a shift towards turf-dominated reefs. While chapter 2 indicates that reasonably severe degradation involving complete loss of kelp over continuous areas is required for turfs to dominate the understory at the expense of other macroalgae, the threshold may be reduced substantially in areas subject to nutrient pollution (Connell et al. 2008).

Biodiversity is also important in conferring resistance of kelp ecosystems to effects of various forms of degradation and can assist recovery following disturbance (Steneck et al. 2002). Biodiversity helps promote diverse ecological functions that may assist with ecosystem stability/recovery (Duffy et al. 2003, Worm and Duffy 2003, Folke et al. 2004, Davenport and Anderson 2007). Diverse assemblages provide functional redundancy, which can help maintain key functions even when particular species are lost (Hughes et al. 2005). The highest richness and diversity of epifaunal invertebrates and fishes tended to occur on larger reefs with the highest density of kelp (chapters 4, 5). Consequently, if there is a relationship between ecosystem stability and diversity (Dayton et al. 1998, Duffy et al. 2003, Worm and Duffy 2003, Folke et al. 2004, Hughes et al. 2005, Davenport and Anderson 2007), declines in kelp cover will likely reduce diversity and thus ecosystem resistance. This positive

feedback effect is likely to see increased risk of shifts to undesirable alternative stable states when stressors result in reduced kelp cover.

6.5 Restoration

Restoration provides an important tool to reverse the effects of habitat decline and maintain biodiversity. The (re-)establishment of kelp on natural and artificial structures is likely to support coastal biodiversity and the associated ecosystem services. However, despite growing interest in the restoration of kelp forests, there are no clear guidelines for best practice (Layton et al. 2020a, Morris et al. *In press*). Although the experiments described in this thesis and those outlined in Layton et al. (2019b) were conducted at relatively small experimental scales, this work highlights that kelp structure has important ramifications for the capacity of kelp patches to be self-sustaining and support the associated communities. Because the survival and growth of microscopic and macroscopic kelp juveniles is often dependent on the ecosystem engineering by adults (Reed and Foster 1984, Layton et al. 2019b), transplanting a sufficient number of adults to restoration sites may be necessary to promote natural recruitment. Layton et al. (2019b) showed that different configurations of transplanted adult sporophytes influenced kelp recruitment. Crucially, transplanting larger and denser patches of adult kelp increased the production and survival prospects of recruits, and there existed a minimum patch size and density of kelp to ensure sufficient recruitment to maintain the kelp patch (Fig. 6.4). This work showed that it is feasible to restore self-sustaining *E. radiata* populations using transplanted adults, and the size and sporophyte density of the transplanted patches will influence kelp recruitment and the likelihood of persistence of the patch.

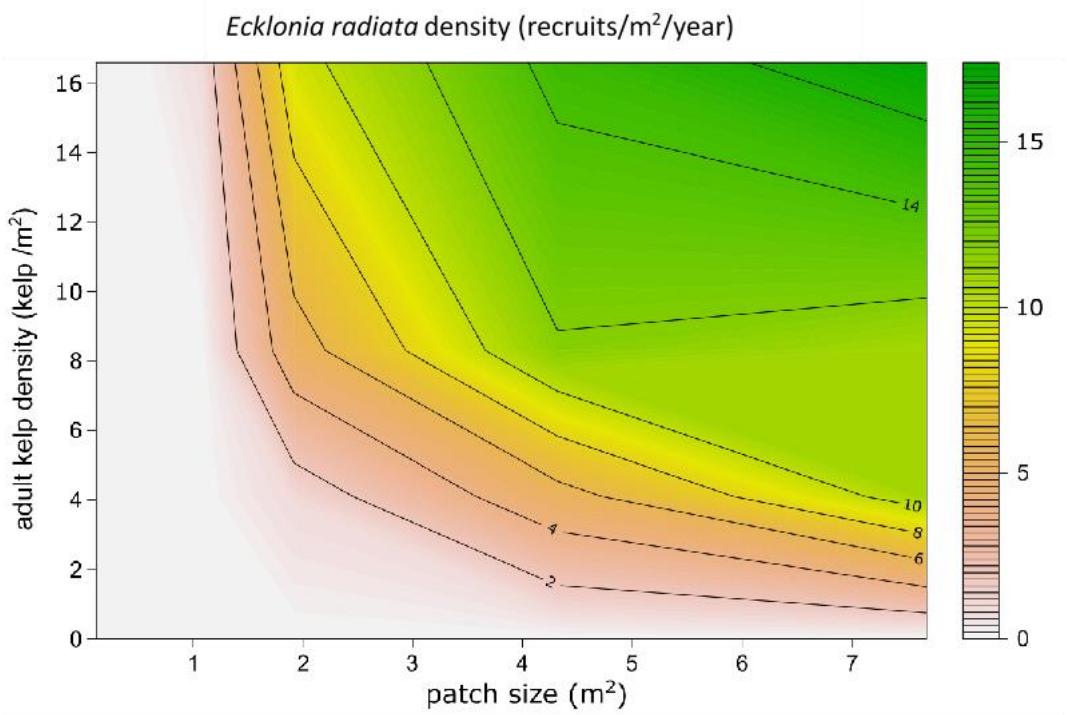

Figure 6.4. Response surface showing the relationship between annual recruitment density of *E. radiata* and the density of adult sporophytes and patch size (after Layton et al. 2019). Annual recruitment necessary to maintain *E. radiata* on these patches is ~ 6 m^{-2} yr^{-1}.

This thesis additionally shows that kelp patch size and density influence the (re-)establishment of kelp-associated communities. As previously indicated transplanting kelp is likely to be extremely effective in reducing the dominance of turf algae and promoting structurally complex benthic habitats. Larger patches supporting high densities of kelp are also likely to promote more productive and diverse communities, and this may benefit the stability of the ecosystem. However, if a major objective of the restoration project is to promote the occurrence of particular target species, alternative structures of kelp might be more effective. For example, large kelp patches supporting low densities of kelp may be most effective in promoting recruitment of native oysters (*Ostrea angasi*) or southern rock lobster (*Jasus edwardsii*) which are ecologically and economically important species. It is not only possible to establish/restore kelp habitat on barren reef; but furthermore, colonisation of

productive and diverse communities is likely to follow rapidly (providing suitable environmental conditions exist). The exact nature of those communities will be determined in part by the size of the patch and density of adult kelp within it. Scaling-up kelp forest restoration projects (beyond experimental scales) is of growing interest and importance and is likely to be necessary to assist with the conservation of these ecosystems (McLeod et al. 2018, Layton et al. 2020b).

6.6 Conclusion

Structure of canopy-forming kelp undoubtedly influences both abiotic and biotic ecosystem properties at the benthos and these effects resonate through communities more broadly. Ecosystem engineering effects elicit complex responses from the associated community, with communities likely to take alternative trajectories depending on the structure of the kelp canopy. Widespread loss of kelp is likely to be required to cause the transition of kelp forest into a turf-dominated ecosystem state, but where this occurs, the associated communities of algae, invertebrates and fishes will differ drastically from those of forested ecosystems. On the other hand, intermediate levels of kelp cover may result in low levels of secondary productivity which may be accompanied by elevated recruitment of *O. angasi* and *J. edwardsii*, but reduced recruitment of some cryptobenthic fishes. There is also likely to be a threshold patch size of approximately $2m^2$, below which the composition of communities is likely to vary drastically from larger patches and support much lower levels of biodiversity. Overall, widespread loss of kelp manifesting as either complete kelp loss of declines in kelp density are likely to have negative effects on the productivity, biodiversity and stability of the ecosystem. On the other hand, the provision of even a small amount of kelp, can promote recruitment of ecologically or commercially important species and increase biodiversity.

There are clearly opportunities and benefits associated with adding kelp to natural and artificial reefs to mitigate the decline of these key habitats and support coastal ecosystems.

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APPENDICES

7.1 Appendix A

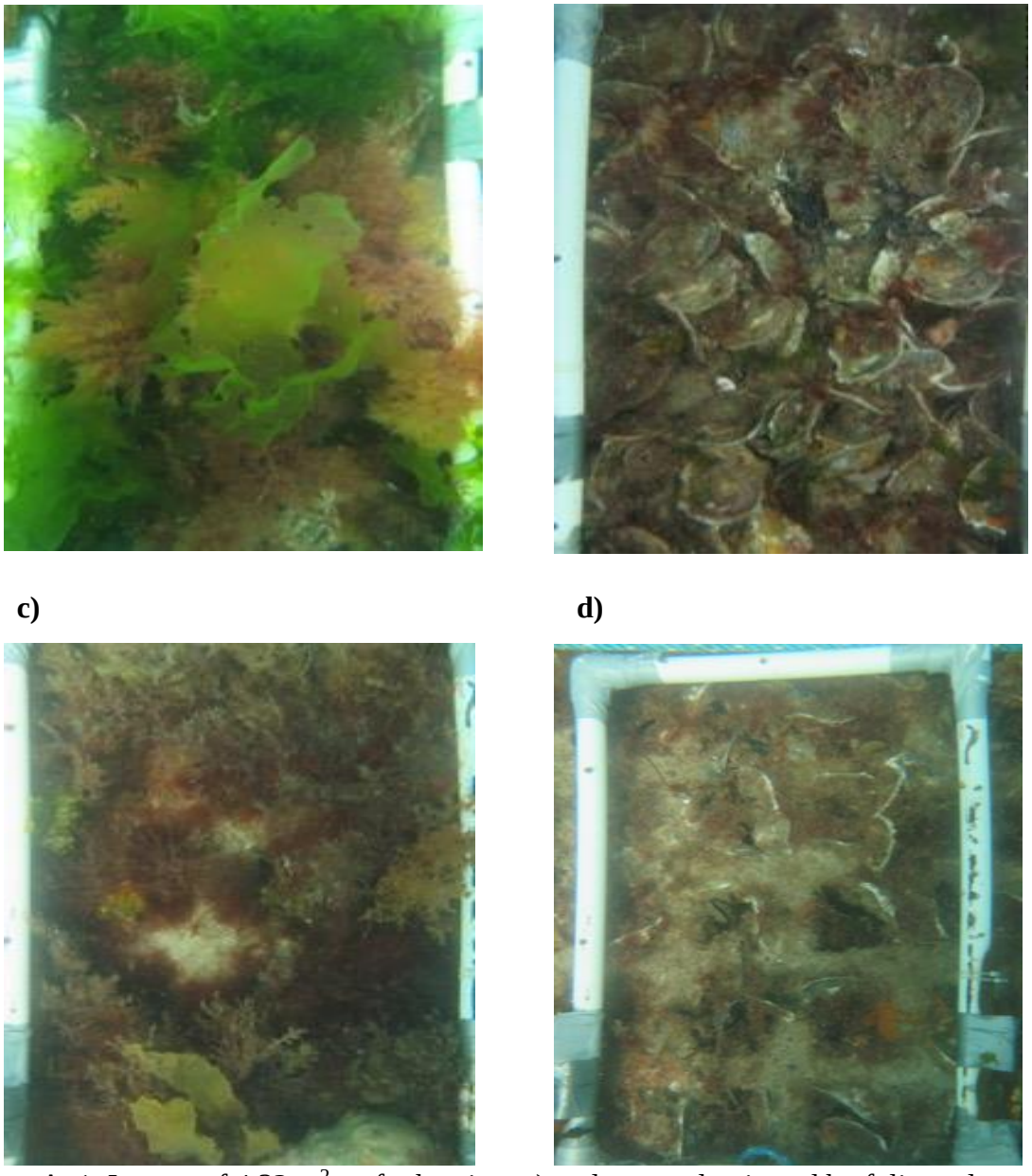
model	factor	SS (df)	F-value	p-value	Post-hoc
BENTHIC RECRUITMENT					
MAY 2015 $(Y)^{0.28}$	$\log_2$(patch size) * kelp density	4.88 (3, 20)	3.42	0.037 *	
MAY 2015 (zero kelp density reefs omitted) $(Y)^{0.49}$	$\log_2$(patch size)	593.76 (1, 17)	58.32	< 0.001 *	
	kelp density	106.58 (2, 17)	5.23	0.017 *	**high** < (**low**, medium)
DECEMBER 2016 $(Y)^{0.58}$	$\log_2$(patch size)	285.87 (1, 23)	12.75	0.0016 *	
	kelp density	775.73 (3, 23)	11.53	< 0.001 *	**zero** < (**low** = **medium** = **high**)
RECRUITMENT TO WATER COLUMN COLLECTORS					
MARCH 2016 $(Y)^{-0.69}$	$\log_2$(patch size)	2.12e-04 (1, 23)	4.14	0.054	
	kelp density	4.68e-04 (3, 23)	3.05	0.049 *	

Table A. 1. Results of ANCOVA models testing the effects of kelp density and patch size on the density of benthic oysters on reefs at 2 times, and the abundance of oyster recruits collected in water column collectors positioned at canopy height in March 2016. Model output is either from full models where there was a *patch size* x *kelp density* interaction or unsaturated models after confirming homogeneity of slopes. Response variable transformations are shown in the *model* column and are given in terms of the untransformed dependent variable, *Y*. Significant p-vales from the ANCOVA are denoted with *. Significant ($p < 0.05$; bolded) and marginally non-significant ($0.05 < p < 0.1$; non-bolded) p-values from post-hoc pairwise tests between different kelp density treatments are shown in the *Post-hoc* column.

		Model optimisation procedure		Hierarchical partitioning	
Nature of predictor variables	Selected predictor variables	Adj. r^2	AIC	Included predictor variables	Independent contribution (%)
OYSTER DENSITY MAY 2015					
Abiotic	Light Deposition	0.68	98.06	Light Deposition Accumulation Flow	77.01 * 6.11 12.21 4.68
Biotic: sessile species	Total algae	0.66	98.19		
Biotic: mobile species	NA				
Abiotic & biotic	Light Deposition Total algae Macroinvertebrate (NS)	0.81	90.73	Light Deposition Accumulation Flow Total algae Macroinvertebrate Fish	38.43 * 5.70 6.27 4.71 38.22 * 5.05 1.61
OYSTER DENSITY DECEMBER 2016					
Abiotic	Light Accumulation	0.74	77.03	Deposition Accumulation Flow Light	8.71 9.21 3.05 79.03 *
Biotic: sessile species	Turf	0.81	66.11		
Biotic: mobile species	NA				
Abiotic & biotic	Turf Macroinvertebrate	0.85	63.95	Deposition Accumulation Flow Turf Macroinvertebrate Fish	5.97 10.12 6.55 50.83 * 24.69 * 1.83

Table A. 2 Summary of regression and multiple regression analyses testing the relationship between abiotic and biotic predictor variables and the density of *O. angasi* at 2 times. The *Nature of predictor variables* column shows whether the predictor variable(s) considered in the model were abiotic, biotic or both. Terms initially selected by the model optimization procedure are shown under the *selected predictor variables* column. The performance of the optimised model is shown in terms of the adjusted r^2 values and Akaike's Information Criterion. Results of the hierarchical partitioning are presented in terms of the independent contribution of each predictor variable to the explained variance in the response variable. Significant contributions are denoted with *. NA denotes no significant predictors identified by analyses.

a) **b)**



c) **d)**

Figure A. 1. Images of 4.32 m^2 reefs showing: a) understory dominated by foliose algae on a reef with medium kelp density, b) *O. angasi* coverage beneath the foliose algae on this reef, c) seaweeds dominated by turfing algae on a reef with no kelp, and **d**) greatly reduced oyster coverage beneath the turfing algae. All images were captured in December 2016.

7.2 Appendix B

ID	Taxon name	ID	Taxon name	ID	Taxon name
MPB/detritus feeder		**Herbivore**		**Filter feeder**	
Order: Amphipoda		**Order: Amphipoda**		**Order: Amphipoda**	
A5	*Tethygeneia*	A3	*Cymadusa*	A12	*Jassa*
A6	*Paradexamine*	A4	*Amphithoides*	A20	*Haplocheira barbimana*
A7	*Tethygeneia*	A11	*Amphithoides*	A33	*Podocerus*
A8	*Paradexamine*	A19	*Gitanopsis*	**Order: Decopoda**	
A9	*Paradexamine*	A25	*Mallacoota*	C7	*Petrolistes elongatus*
A10	*Stenothoe*	A30	*Melitidae*	**Class: Bivalvia**	
A15	*Aora*	A31	*Dulichiella*	Bi1	*Ostrea angasi*
A16	*Gammaropsis*	**Order: Isopoda**		Bi2	*Electroma geogiana*
A17	*Photidae*	I1	*Sphaeromatidea*	Bi3	*Musculus nanus*
A21	*Jassa*	**Order: Decopoda**		Mu	*Mytilus edulis*
A32	*Amphithoides*	C5	*Notomithrax*	Bi5	*Barnea sp.*
A35	*Seba*	**Class: Gastropoda**		Bi6	*Mimachlamys asperrimus*
A36	*Iphimedia*	SN13	*Zafra atkinsoni*		
Ca1	*Caprella*	SN10	*Mitrella*		
Order: Tanaidacea		**Class: Polyplacophora**			
A13	*Nototanais*	chiton	*Chiton*		
Order: Isopoda					
A14	*Zeuxokoma*				
Carnivore		**Detritivore**		**MPB feeder**	
Order: Isopoda		**Order: Amphipoda**		**Order: Amphipoda**	
Ca2	*Mesanthura*	A1	*Amaryllis macrophthalma*	A22	*Aora maculata*
Order: Decopoda		A2	*Parawaldeckia*	**Class: Gastropoda**	
C4	*Halicarcinus ovatus*	**Order: Decopoda**		SN2	*Phasianotrochus apicinus*
SL	*Galathea australiensis*	C1	*Planes minutus*	SN3	*Phasianotrochus eximius*
S1	*Palaemon dolospinus*	C2	Megalopa larva	SN5	*Phassianotrochus rutilis*
S2	*Palaemon intermedius*	HC	*Pagurixus handrecki*	SN8	*Phasianella australis*
S3	*Chlorotocella spinicaudus*	**Class: Gastropoda**		SN10	*Ballastraea aurea*
S5	*Alpheidae*	SN1	*Nassarius pyrrhus*	nudi	unidentified nudibrach
S7	*Latreutes compressus*	SN12	*Cacozeliana granarium*		
S8	*Hippolyte*	**Class: Polychaeta**			
Class: Gastropoda		P2	Syllid polychaete	DBR: damaged beyond recognition	
SN9	*Sassia*	**Class: Ophiuroidea**			
Class: Polychaeta		BS	*Amphipholis squamata*		
P1	Chrysopetalid sp.				

Table B. 1. List of epifaunal invertebrates observed in rope fibre and natural habitats grouped by feeding strategy. MPB = microphytobenthos. Taxon ID is used in Figs. 4.4 and 4.5.

factor	SS (df)	pseudo-F	p-value	significant comparison
RFH				
reef size group x position	7411 (1, 40)	7.20	0.001 *	
RFH (SMALL ONLY)				
kelp density	5916 (3, 24)	2.05	0.064	
position	3162 (1, 24)	3.29	0.034 *	
RFH (LARGE ONLY)				
kelp density	8172 (3, 16)	2.41	0.005 *	zero ≠ (low, med, high)
position	8460 (1, 16)	7.49	0.001 *	
RFH (CENTRE ONLY)				
size group x kelp density	6686 (3, 20)	2.22	0.012 *	
RFH (NORTH ONLY)				
size group	5378 (1, 20)	5.11	0.005 *	
kelp density	5368 (3, 20)	1.70	0.132	
NH				
kelp density	7262 (3, 20)	2.06	0.007 *	zero ≠ (low, med, high); low ≠ high
reef size group	8956 (1, 20)	7.64	0.001 *	

Table B. 2. Summary of significant effects from PERMANOVA models testing the effects of kelp density, reef size group and (when relevant) position of rope fibre habitats (RFH) on the community structure of epifauna associated with RFH and natural algal habitat (NH) on reefs of different size supporting different kelp densities. Where interactive effects were detected, the structure of epifaunal communities associated with different subsets of reefs (indicated in brackets) was assessed. Significant post-hoc pairwise comparisons ($p < 0.05$) are indicated in the significant comparisons column.

factor	SS (df)	pseudo-F	p-value	significant comparison
RFH				
reef size group x position	7411 (1, 40)	7.20	0.001 *	
RFH (SMALL ONLY)				
kelp density	5916 (3, 24)	2.05	0.064	
position	3162 (1, 24)	3.29	0.034 *	
RFH (LARGE ONLY)				
kelp density	8172 (3, 16)	2.41	0.005 *	zero ≠ (low, med, high)
position	8460 (1, 16)	7.49	0.001 *	
RFH (CENTRE ONLY)				
size group x kelp density	6686 (3, 20)	2.22	0.012 *	
RFH (NORTH ONLY)				
size group	5378 (1, 20)	5.11	0.005 *	
kelp density	5368 (3, 20)	1.70	0.132	
NH				
kelp density	7262 (3, 20)	2.06	0.007 *	zero ≠ (low, med, high); low ≠ high
reef size group	8956 (1, 20)	7.64	0.001 *	

Table B. 3. Summary of ANCOVA models testing the effects of kelp density, reef size and when relevant fibre habitat (RFH) position on productivity:biomass (P:B) with RFHs and natural algal habitat (NH). Model output is from the unsaturated models after confirming homogeneity of slopes. Response variable transformations are shown in the model column. The covariate reef size was $\log_2$ transformed. Significant p-values from the ANCOVA are denoted with ***.** Significant post-hoc pairwise comparisons are indicated in the post hoc column.

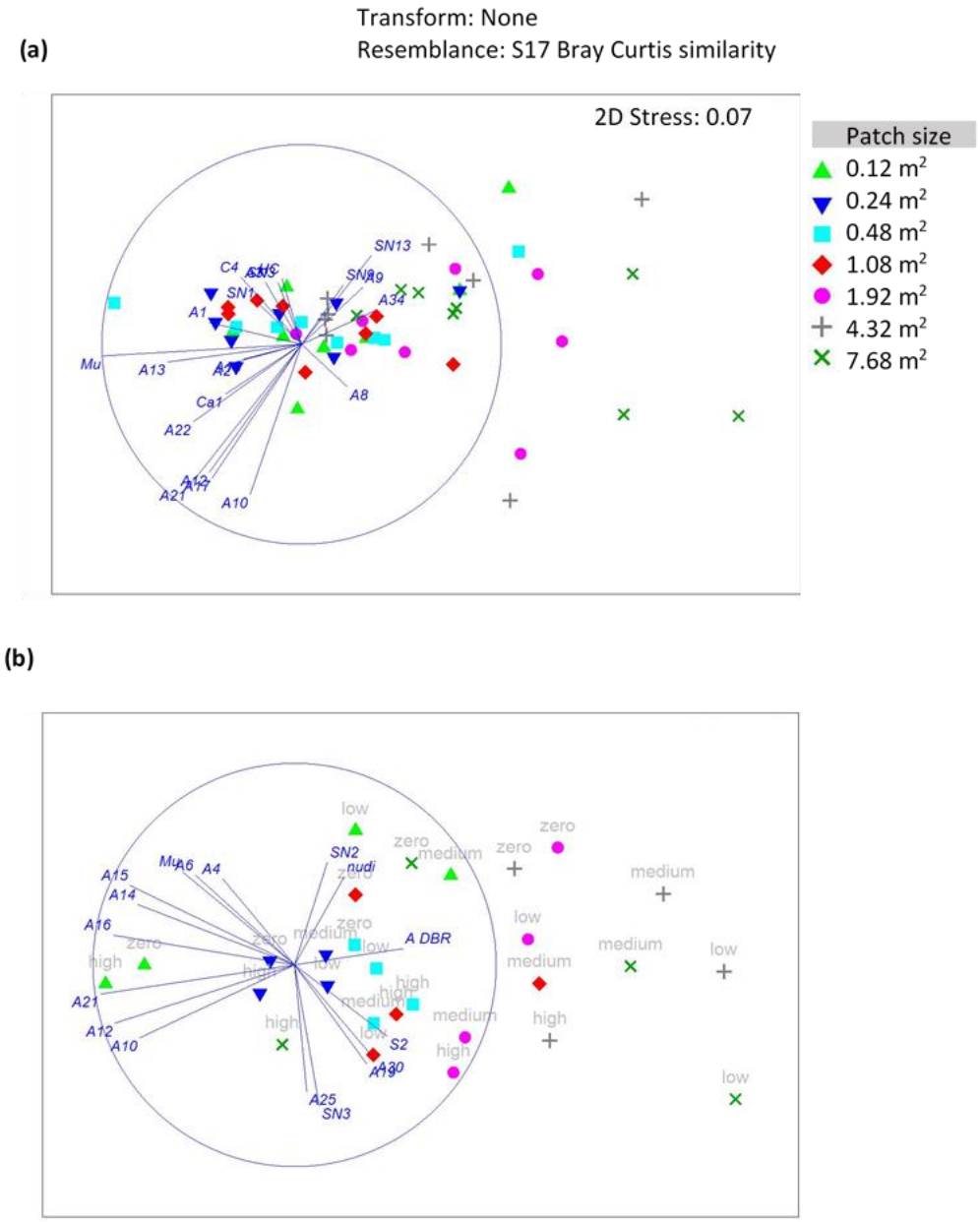


Figure B. 1. MDS of epifaunal invertebrate communities associated with a) rope fibre habitat (RFH) and b) natural algal habitat (NH) used to determine reef size groups for PERMANOVA analysis. Vector overlay depicts species with Spearman correlations > 0.3 and > 0.5 for a and b respectively. Refer to Table 1 for species ID.

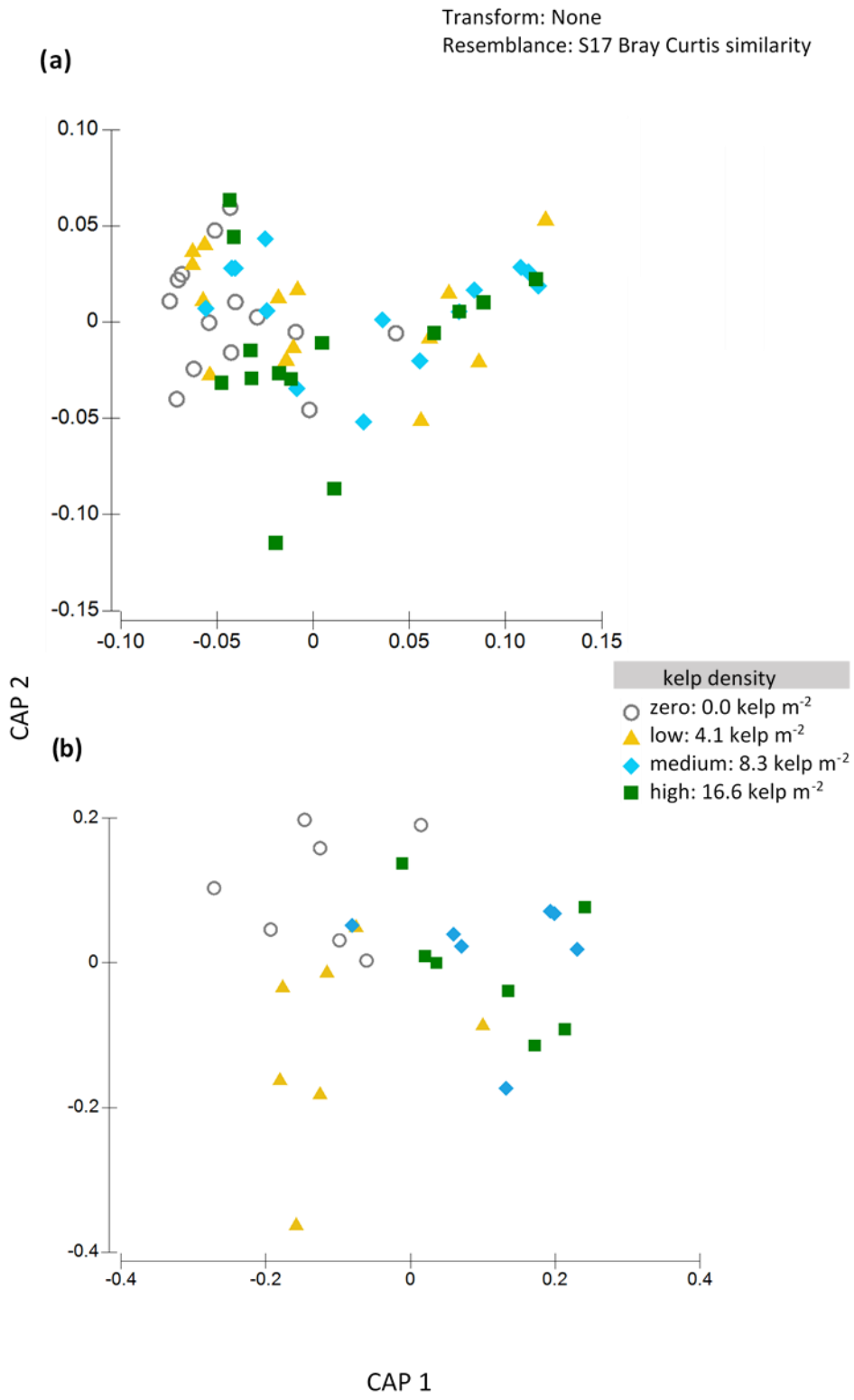


Figure B. 2. Canonical analysis of principal coordinates (CAP) of epifaunal invertebrate communities associated with a) rope fibre habitat (RFH) and b) natural algal habitat (NH), maximizing separation across kelp density.

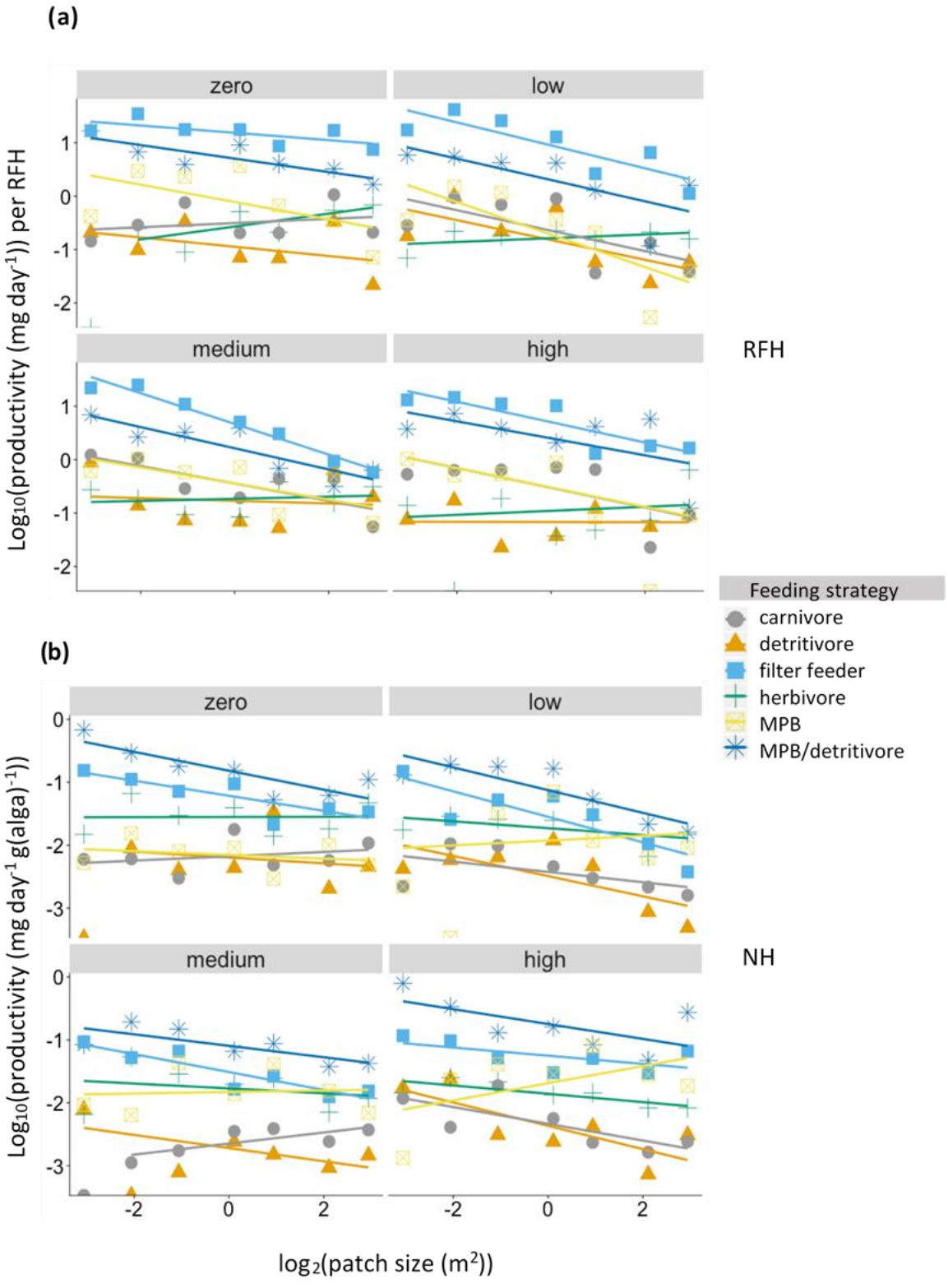


Figure B. 3. Secondary productivity of epifauna with different feeding strategies from reefs of different size and kelp density determined through analysis of rope fibre habitats from the centre of each reef, and natural algal habitat.

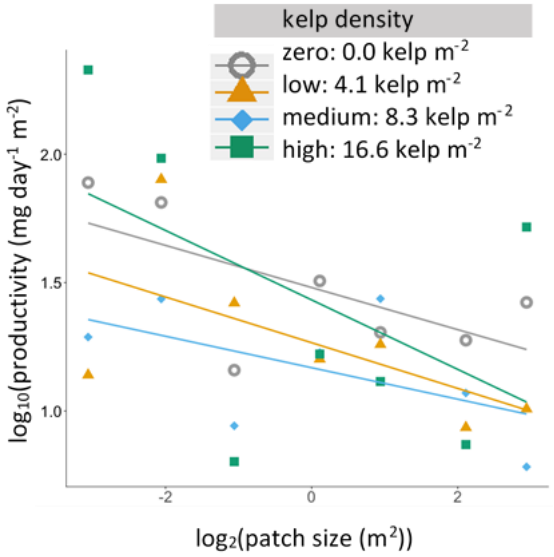


Figure B. 4. Secondary productivity associated with natural algal habitat (NH) per m^2 on reefs of different size (shown in m^2) and kelp density (expressed as zero, low, medium, high).

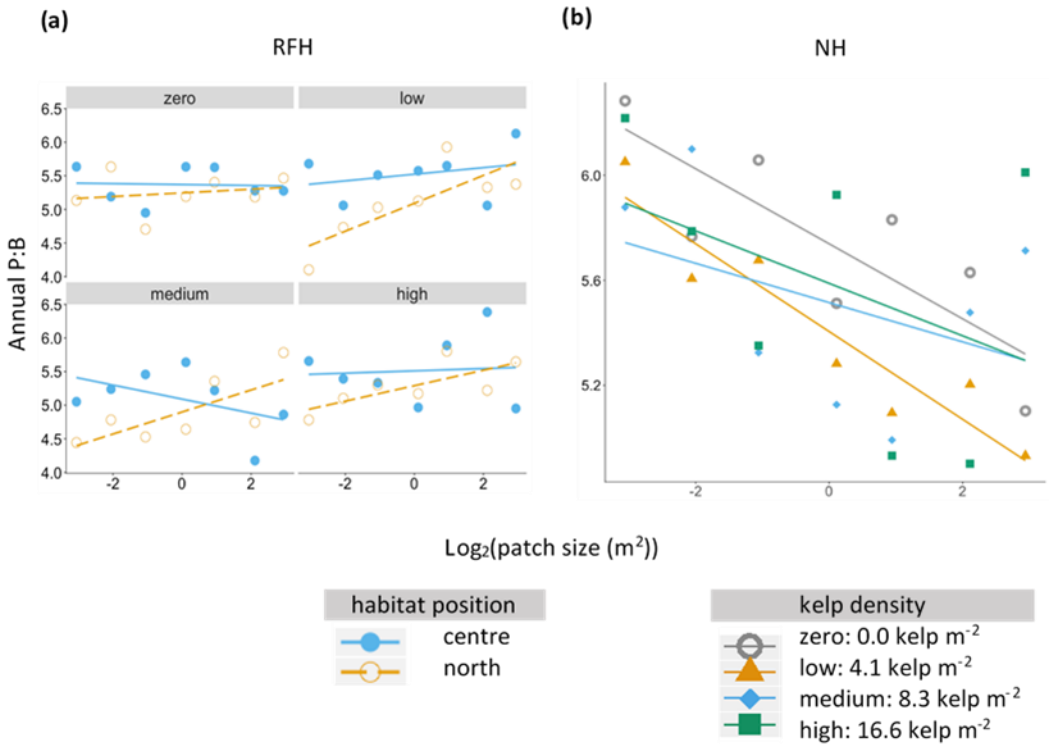


Figure B. 5. Productivity:biomass (P:B) of epifauna associated with rope fibre habitats (RFH) positioned either on the northern (light exposed) edge (N) or the centre (C) of reefs of different size (shown in m^2) and kelp density (expressed as zero, low, medium, high). **b)** Productivity:biomass (P:B) of epifauna associated with natural algal habitat on reefs of different size and kelp density.

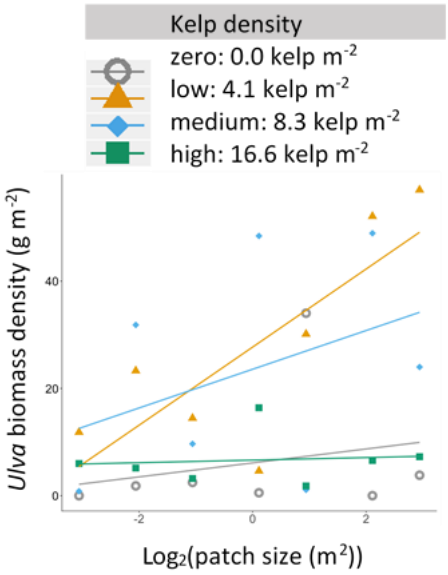


Figure B. 6. Biomass density of Ulva sp. from reefs of different patch size and kelp density (based on dry weight).

7.3 Appendix C

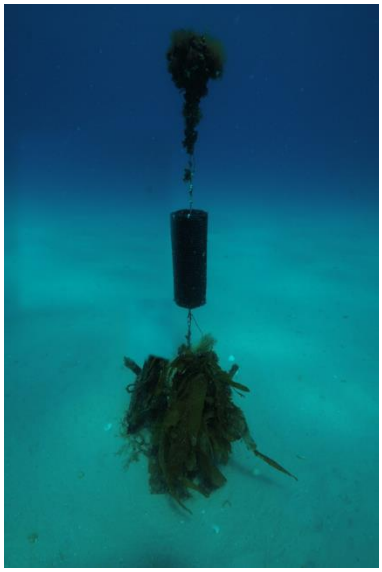


Figure C. 1. Image showing a larval fish collector on the smallest (0.12m2) sized reef.

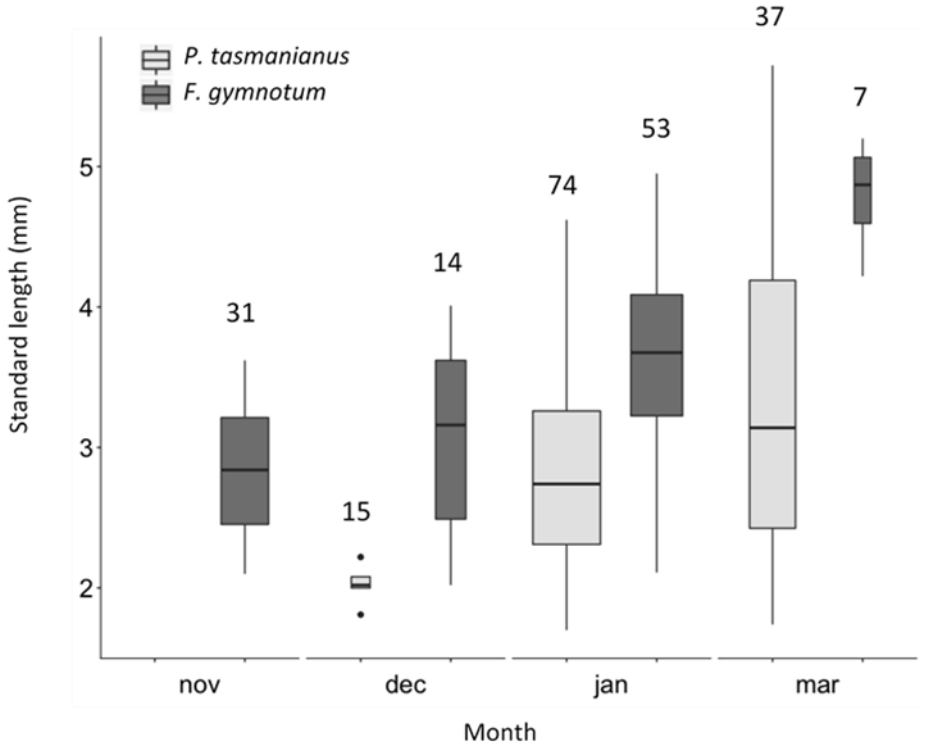


Figure C. 2. Size (standard length) of *Parablennius tasmanianus* and *Forsterygion gymnotum* recruits collected in SMURF fish collectors, pooled across experimental reefs at four times between November 2015 and March 2016. Box shows the median and the upper and lower quartiles, and whiskers extend a further 1.5 x the interquartile range. Numbers on plot and plot thickness indicates number of recruits collected.

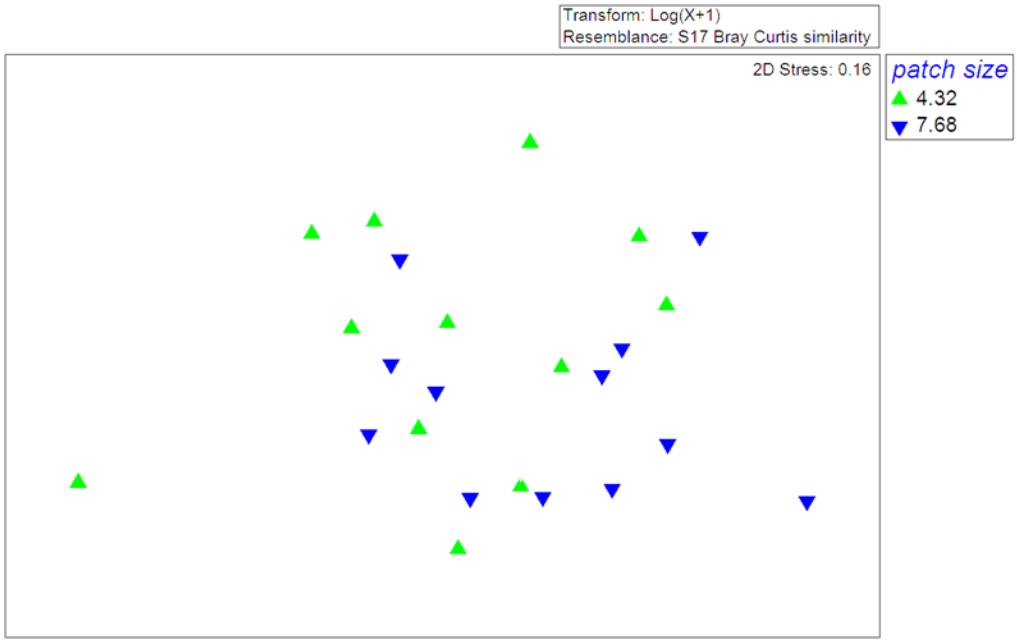


Figure C. 3. MDS of fish community structure expressed as the density of each species observed on the two largest reefs (4.32m^2 and 4.32m^2) reefs of different kelp densities at three stages of the experiment, highlighting the effect of patch size.

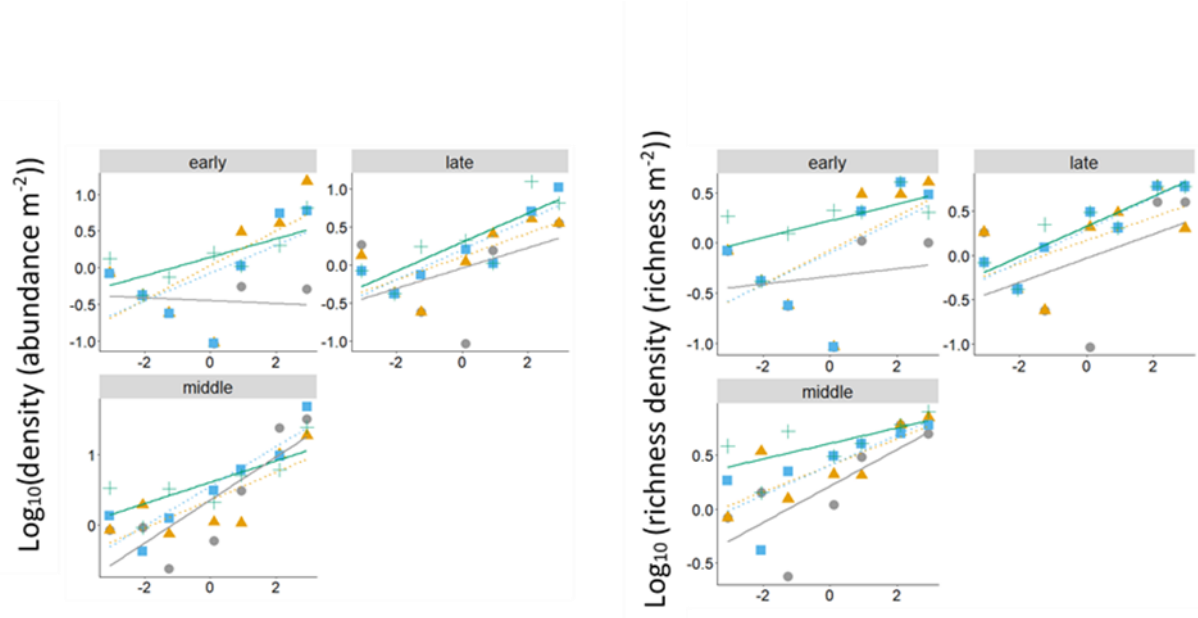


Figure C. 4 a) log density (abundance/patch size) and b) log species density (species richness/patch size) of fishes across reefs of different patch size and kelp density at three stages of the experiment (early: spring 2015, middle: autumn 2016, and late: spring 2016). Solid lines highlight comparisons between reefs supporting zero kelp and reefs supporting a high density of kelp.